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CONTRIBUTIONS TOWARD A RECLASSIFICATION
OF THE FORMICIDAE. II. TRIBE
ECTATOMMINI (HYMENOPTERA)

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No. 5 — *Contributions toward a Reclassification of the Formicidae. II. Tribe Ectatommini (Hymenoptera)*

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INTRODUCTION

This section deals with a large group of species in the subfamily Ponerinae, including most genera formerly placed in the old tribes Ectatommini, Paraponerini and Proceratiini. These genera are now grouped in a single, broadened tribe Ectatommini.

The previous "standard" classification of the subfamily Ponerinae, stabilized by Emery in his 1911 fascicle of the Genera

Insectorum, was altered but little when Wheeler made additions to it in his generic key of 1922. In 1911, Emery's system was a great advance over older arrangements in many respects, but the flood of description in more recent years has swamped it completely. Since basic classification has been neglected for so long a time, we are now faced with the necessity of constructing a completely new system. I have undertaken to make this replacement through the revision of tribes or similar-sized taxa, one at a time, and the publication of the results of tribal units. Thus, at least some of the results will be available for the necessary use and testing by other specialists long before a full subfamily revision could possibly be completed. It is hoped, however, that after the series of tribal sections is complete, there will be an opportunity to make final adjustments and to construct a grand key to the genera of the subfamily.

The Emery-Wheeler classification of the Ectatommini,
Paraponerini and Proceratiini, with a summary
of the changes here proposed

Emery recognized the Ectatommini, Paraponerini and Proceratiini as separate tribes within the Ponerinae, but the present evidence of their close relationship seems to make any such tribal division unnecessary and unrealistic. The Paraponerini include a single genus with one species, and the conclusion reached after a close consideration of the characters of all castes of *Paraponera clavata* is that tribal rank was granted in this case almost solely on the basis of the extraordinarily large size of the individuals of the species. Admittedly, *Paraponera* is unique in a couple of other respects as well, but its ectatommine relationships are so clear in its habitus in all adult castes, in its behavior, and in details of morphology such as the male genitalia (Weber, 1946) that it can no longer be considered as more than a slightly aberrant ectatommine.

The Proceratiini have even less claim to tribal separation from the Ectatommini, at least on adult characters. In fact, there is grave difficulty to be encountered in separating *Proceratium* of the Proceratiini from *Heteroponera* of the Ectatommini even at the generic level. The only doubts here rest on the unusual

nature of the proceratiine larvae, but then these are known for only a few species in one genus, *Proccratium*, and for none of the *Heteroponera* species. The Ectatommini appear to make up one reasonably clearcut tribe with these inclusions.

Emery divided his tribe Ectatommini into two subtribes: Ectatommini, *sensu stricto* and Typhlomyrmicini. It has already been shown that two of the three genera of the Typhlomyrmicini (*Typhlomyrmex* Mayr and *Prionopelta* Mayr) are members of different ponerine tribes, and that they should be excluded from consideration under the Ectatommini (Brown, 1950, 1953a, 1953b). The third genus in this subtribe is *Rhopalopone* Emery, the species of which have been consistently characterized, and wrongly so, as lacking median teeth on the tarsal claws. In fact, such teeth are present in most, if not all species that have been placed in *Rhopalopone*, and a separation between these species and others now placed in *Gnamptogenys* is considered impossible. The synonymy of *Rhopalopone* with *Gnamptogenys* removes the last genus from subtribe Typhlomyrmicini, and thus removes all necessity for recognizing this subdivision any longer. I had considered retaining Paraponerini and Proceratiini as subtribes in the Ectatommini, *sensu lato*, but in the end this subdivision seemed misleading and an unnecessary complication to the system, and it was rejected.

Among the genera of the ectatommines, *Acanthoponera* is worthy of generic rank on present evidence. The erstwhile subgenus *Anacanthoponera* is a straight synonym of genus *Heteroponera* Mayr (Brown, 1952c), and *Paranomopone* is also considered to belong to *Heteroponera* in this revision. *Aulacopone* is retained as a genus, at least until more is known about it. *Rhytidoponera* is retained as a separate genus, also, and *ChalcoPONera* is included as a synonym (Brown, 1953b). *Ectatomma* is considered to be a genus apart from *Gnamptogenys* and the remainder of its erstwhile subgenera. *Gnamptogenys* is preserved as a separate genus and, despite long and earnest attempts to find some basis for separation of two or more generic or subgeneric groups, I have been forced to place in its synonymy a number of generic and subgeneric names, including some much-used and familiar ones: *Holcoponera*, *Stictoponera*, *Emeryella*, *Parcetatomma*, *Rhopalopone* and *Alfaria*, as well as some less

well known names: *Whecleripone*, *Spaniopone*, *Poneracantha*, *Barbourella*, *Opisthoscyphus*, *Tammoteka* and *Commateta*. Of the genera formerly included in the Proceratiini, *Probolomyrmex* Mayr and its probable synonym *Escherichia* Forel have been transferred to tribe Platythyreini (Brown, 1952a). *Proceratium* has been found to grade into *Sysphingta* (*Sysphincta* of authors), so synonymy is indicated here, with *Proceratium* the prior name. For similar reasons, *Discothyrea* becomes the senior synonym of *Prodiscothyrea* and *Pseudosysphincta*.

The Ectatommini come in this way to contain nine reasonably distinct genera: *Acanthoponera*, *Heteroponera*, *Rhytidoponera*, *Paraponera*, *Ectatomma*, *Aulacopone*, *Gnamptogenys*, *Proceratium* and *Discothyrea*.

Characters and Relationships among the Genera of Ectatommini

Taxonomy in the Ectatommini is chiefly dependent upon the characters of the adult worker, for this is the caste most commonly collected and described, and the one with the clearest differentiation of external morphological features. Queens follow workers in generic and specific characters for the most part, and many of them are present only as wingless ergatoids scarcely distinguishable from workers, or perhaps not distinct at all (*Rhytidoponera* spp.). The degree of caste divergence in the female sex is moderate, therefore, to nearly or quite non-existent.

The males show marked divergence from the females, but sexual dimorphism is not as strong as among some other formicid genera, even in the Ponerinae. The size is usually a little smaller than the corresponding female, and the sexual differences are otherwise much as seen in other ponerines. Males are rare in collections, and often are not in association with workers or females in the cabinet. Within the tribe, the males show greater conservatism in morphology than do the workers and queens, and, with few exceptions, the male characters are not known to furnish clear generic distinctions. The males of a species may often be distinguished by characters reflecting those shown more strongly by its workers and queens, so that males in association with workers are normally determined through the workers.

Perhaps a study of such characters as wing venation, genitalia, palpal segmentation, antennal form, and so on, will eventually furnish good male distinctions independent of those seen in the workers, but such a study must await much more complete collections. Some male characters will be mentioned below for the genera in which this caste is known.

The larvae of the ectatommines are also relatively incompletely known, and before the pioneering work of the Wheelers on the ponerine larvae (1952a: 117-139, pls. 2-5; 1952b, 657-661), there was virtually nothing in print of any value for morphological or systematic purposes. The larval findings agree in most respects at the generic level with the new classification adopted here. The Wheelers have been hampered in their work by a lack of material in some of the rare, but taxonomically critical genera. It is hoped that those specialists having access to the material needed to fill these gaps will see that larval specimens are forwarded to colleagues ready to study them.

At the present time, the relationships of the Ectatommini are not entirely clear, but it does seem likely that tribes Ponerini and Platythyreini are approximately cognate members of the Poneroid Complex (Brown, 1954a). There is evidence in the form of the male alitrunk, wings and genitalia, in the integumental consistency, proventricular structure, propodeal form and armament of all castes, and especially in the structure and proportions of the post-propodeal segments and their organs, that subfamily Myrmicinae arose from an ectatommine ancestor, and this supposition is strengthened by the characteristics of the fossil *Agroecomyrmex* Wheeler, which seems to provide a near-ideal intermediate form. These speculations on ectatommine connections seem reasonably safe to put forward at this time, but beyond this, nothing is gained by suggesting detailed relationships in the absence of the necessary comparative morphological data.

Within the tribe Ectatommini, the genus surviving with the greatest number of primitive characters appears to be *Acanthoponera*. This genus retains (in the female castes) the primitive palpal formula for ants: 6 maxillary, 4 labial segments. *Acanthoponera* also bears the strong extra tooth on each tarsal claw found in the most primitive ponerines and myrmecines, and

the alitrunk has a complete and possibly flexible articulation between pro- and mesonotum. It is interesting to note that this genus, like some other genera primitive within their respective tribes, is fitted with the large eyes and strong spinous armament marking an arboreal forager, and it is now known that *Acanthoponera* is in fact a nocturnal arboreal forager. All of the characters mentioned above, which happen to be generalized conditions for the ants as a family, oppose the tendency toward ankylosis of antennae, palps, and alitrunk. Other trends that cause the body to become more compact, such as reduction of spinous armament, and also the reduction of the eyes, accompany the ankylotic tendencies more or less consistently, apparently in correlation with a change from arboreal through ground-foraging to hypogaeic or otherwise cryptobiotic habits of the ants. This trend is clearly observable within the single myrmicine tribe Dacetini, as it is within the ectatommines. The frequent association of arboreal, tropical forms with characters generally considered to be the generalized ones for ants indicates a greater likelihood that the forested tropics were a more prolific evolutionary source in terms of major groupings than were the more arid regions usually cited as important to formicid major-group evolution (see also Bernard, 1948).

Acanthoponera is advanced in one respect, however; the known winged specimens of both sexes lack the anal lobe of the hind wing. All other ectatommines lack this lobe, too, except *Paraponera* and *Ectatomma*, each of which has well-developed lobes in all of the species so far seen. The loss of the anal lobe may mark a monophyletic lineage within the ectatommines, since there are additional grounds for linking most of the genera without it. *Heteroponera*, for instance, can be derived directly from *Acanthoponera*, and *Rhytidoponera* is very closely related to *Heteroponera*, especially through the species *H. relictata*. Judging from the original description and figures, *Aulacopone* also seems to be close to *Heteroponera*, but this needs to be confirmed by a new examination of the type or additional material that may have accumulated in collections. *Proceratium* and *Discothyrea* seem, on the basis of adult characters, to be closest to *Heteroponera*, and the amber species *Bradoponera mcieri* (Mayr, 1868; Wheeler, 1914) looks like a reasonable intermediate step in this line. A

comparative study of the larvae in this group is needed in order to decide how real the link between the "proceratiines" and *Heteroponera* may be.

The large and heterogeneous *Gnamptogenys* group is difficult to relate precisely to other genera, but it seems closer to the *Acanthoponera-Heteroponera* line than to *Ectatomma*, despite previous placements to the contrary. This leaves *Ectatomma* and *Paraponera* as offshoots from near the base of the ectatommine stock. The poorly-known Baltic Amber genus *Electroponera* Wheeler may represent an intermediate link between these genera and the main line of the tribe.

Two other fossil species, *Ectatomma europaeum* Mayr (1868) and *Archiponera wheeleri* Carpenter (1930; see also Wheeler, 1930) appear to belong either in or very close to *Gnamptogenys* in the present broad sense. *Gnamptogenys europaea* (Mayr) is the **new combination** for the Baltic Amber species, proposed tentatively on the basis of the original description of the winged female and Wheeler's (1914) characterization of the supposed male of this species. As Wheeler suggests, *Archiponera* may be near the *schmitti* group of *Gnamptogenys* (= *Emeryella*), although the state of preservation of the fossil, from the Oligocene Florissant Shales, leaves something to be desired. All of the fossils are interesting chiefly in that they show a widely diversified group of ectatommines to have existed at least as far back as the Oligocene, in northern areas from which the tribe is now absent completely or nearly so.

Geographical Distribution of the Genera

The pattern of ectatommine distribution is today essentially a peripheral one. The relatively large-bodied, epigaecially-foraging stocks are developed almost exclusively in the Neogaecic and Indo-Australian (especially Australian) Regions, where they are largely confined to tropical and warm temperate climates. From this, it will be clear that by "peripheral," I mean peripheral to the larger continental land masses of Eurasia, North America and Africa. However, since the presence of epigaecially-foraging stocks is clearly indicated in the fossil record of the Northern Hemisphere, we know that the distribution of ectatommines has not always been an essentially fringing one, and

we suspect that the group may have had its principal source of evolutionary change in the central regions during earlier times. In the same central regions now, we find only a thin and discontinuous representation of specialized cryptobiotic types, like the species of *Proceratium* and *Discothyrea*, managing to survive by remaining ecologically unobtrusive.

Among the epigaeic genera, *Paraponera*, *Ectatomma*, and *Acanthoponera* are restricted to the New World in warm climates and are all clearly distinct from Old World members of the tribe. *Heteroponera*, a rather conservative stock, is distributed rather widely in both the Australian and Neogaic Regions, but shows no obvious tendency to split into two groups following the geographical separation. *Rhytidoponera* is a very successful and luxuriantly radiating stock of the Australian Region; it halts at New Caledonia in the east, but ranges widely through Melanesia to the islands stretching from Timor to the southern Philippines on the west. *Rhytidoponera* looks as though it may have originated in the Australian region from some *Heteroponera*-like stock. *Aulacopone* has so far been reported only from the type locality in Russian Armenia; obviously, it has cryptobiotic tendencies.

Gnamptogenys is a large and wide-ranging genus, occurring both in the Indo-Australian Region (Ceylon and western China to Fiji, but not known from Australia, New Caledonia or New Zealand) and in the New World (Argentina to Texas, West Indies). This genus can be grouped into different lines, more or less equivalent to the genera and subgenera here synonymized, and reflecting in part the separation between New and Old World, as well as the water gap between archipelagic and continental faunas. However, these lines have not lost their associations through intergradient species, and these intergradient species, most of which exist in the New World, show that the lines still belong to the same genus at the present time level. It thus appears that *Gnamptogenys* must represent the last major radiative burst of the epigaeic ectatommines, already replaced in its center of origin, and unable to expand in the direction of Australia because of the powerfully-developed *Rhytidoponera* stock already present in that country.

Of the two predominantly cryptobiotic genera, *Proceratium* and *Discothyrea*, the former tends to have a more northerly range, while the latter is found more to the south. Both genera occur in the tropics, often in the same areas, and there are broad overlaps in range in both northern and southern temperate areas. *Discothyrea* is best developed and most abundant in tropical America and southward to Argentina, in the Australian region, and in central and southern Africa. *Proceratium* reaches a peak of abundance and diversity in the warmer parts of the Holarctic Region, wherever sufficient moisture exists, and this genus is well represented in the East Indies. In Central America there are three rare species, and two species have reached into the eastern tropical forest belt of Australia as far south as Brisbane. Another species has colonized Fiji. Two species are known from tropical Africa. This apparent tendency of the two genera to have complementary ranges outside the tropics is very interesting, but we know so little about the habits, particularly the food habits, of these ants that it is not now possible to say whether the tendency is adaptive in promoting avoidance of competition between the groups.

The presence of two endemic ectatommine species of different stocks (*Heteroponera* and *Discothyrea*) in New Zealand (out of a total of at most ten ant species endemic in New Zealand), and of moderately to highly diverse native representations of the tribe in southern South America, southern Australia, the Solomons, Fiji and New Caledonia, speaks for the age of the group. Few ant tribes can match this "extralimital" range, and of those that do, the Amblyoponini share an archaic aspect and a poverty of representation in the Ethiopian and other "central" land masses. Bearing in mind the Oligocene fossil traces and the lack of good ant fossils in earlier levels, it seems likely that the Ectatommini go back to or slightly beyond the beginning of the Tertiary. It may be guessed that the present peripheral contraction of the Ectatommini is due, at least in part, to the pressure of the rising Myrmicinae. The beginnings of a diversified myrmecine fauna are seen in the Baltic Amber, as well as in the Florissant Shales, but true members of the most potent myrmecine genera, *Pheidole* and *Crematogaster*, do not appear in these formations, nor even in later (Miocene) strata.

Treatment of Species-Level Taxonomy

The primary purpose of this section is to revise the generic classification of the Ectatommini, but in the course of the necessary review of the literature and authentic material of nearly all of the named forms, many species-level situations were found to require synonymy, adjustment or amplification. Also, among a number of previously undescribed species seen, certain ones were found to affect generic concepts by broadening them or by bridging what were formerly thought to be natural gaps. For these reasons, descriptions of a few new species were necessary to the primary purposes of this work; descriptions of still other species that do not affect generic concepts as significantly have been omitted here, though it is hoped that these can be treated elsewhere.

The compilation of a work of this sort also inevitably includes a miscellany of new or under-appreciated data referring to morphology, distribution, behavior, ecology, and variation, of a kind lacking in the literature for most of the forms in this tribe. In order that the required documentation backing the present major conclusions, and also the subsidiary information, should neither clutter the presentation of the generic data nor become a lost by-product, I have relegated most of this matter to an appendix, where the items are listed consecutively against boldface numbers corresponding to the indicator numbers placed in brackets in the text.

After synonymy and general remarks, there are listed for each genus the currently recognized species as far as known to me. Synonyms listed as such in Emery (1911) are omitted here. Each species is followed by author, date and page of original reference; the sources are listed more fully at the end of the paper.

Of the many forms treated until now as varieties or subspecies, some are rather obviously synonyms, and are treated as such with a minimum of discussion. Varieties and subspecies of unclear status are listed arbitrarily as species, since I feel that these names will eventually stand or fall as species or as infraspecific variants not worthy of formal nomenclatorial recognition (Wilson and Brown, 1953; Brown and Wilson, 1955). I should perhaps emphasize that the listing of former infraspecies names as species

here implies no real conviction on my part that these entities are really worth the distinction; actually, I feel that most of such names will be revealed as synonyms when the proper study of their types has been made.

The capital letters placed in parentheses before each specific name indicate the kind of evidence upon which the present generic placement is directly based.

(T) indicates that type material, nidotypes, reliably type-compared material, or similarly authentic specimens have been examined, in most cases by myself; rarely, examination has been made by other myrmecologists.

(P) means that material identified from reasonably good descriptions, or from other satisfactory evidence, has been examined and is thought to be correctly determined.

In cases where the species is not seriously questioned, but no specimens referable to it have been seen, or if specimens seen cannot be satisfactorily verified as to identity, no entry has been made before the species name.

(?) signifies that, in my opinion, the species is inadequately described for purposes of distinction and that its taxonomic status is doubtful.

The species lists have been based on various myrmecological compendia and basic papers, and were checked against Emery's Genera Insectorum list and the Zoological Record, 1908 through 1953. References through 1957 are included so far as I am aware of them. I shall consider it a great favor if readers will send me notice of the inevitable omissions for inclusion in a corrective supplement.

Key to the genera of Ectatommini, based on the workers

1. Size very large, head width across eyes over 3.6 mm.; hypopygium with an upwardly-directed comb of fine teeth on each side (Neotropical)

Paraponera Fr. Smith

Size much smaller, head width across eyes under 3.6 mm.; hypopygium without lateral combs 2.

2. Lobes of frontal carinae more or less sharply raised (sometimes vertical and fused together), leaving the condylar bulbs of the antennae completely or nearly completely open to dorsal full-face view (Figs. 1, 23-25,

46, 48). Small, compact chiefly cryptobiotic forms, usually ferruginous in color and with reduced eyes (Figs. 45, 47) 3.
 Lobes of frontal carinae horizontal or at most feebly raised, covering or nearly covering the condylar bulbs of the antennae (Figs. 12, 36, 41, 43, 44). Mostly epigaeic foragers, but a few species are cryptobionts with characters to match 4.

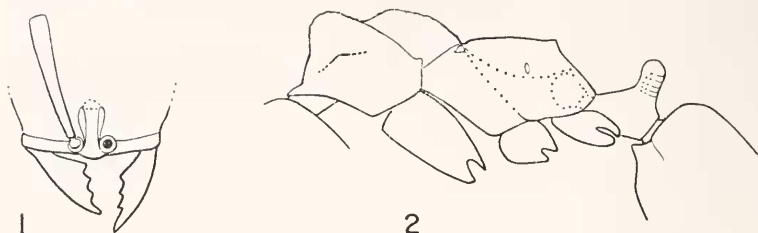


Figure 1. *Proceratium arnoldi* Forel, syntype worker, dorsal view of anterior part of head, from a sketch by Dr. G. Arnold. Figure 2. *Ectatomma ?confine* Mayr, worker (Lancetilla, Tela, Honduras), side view of alitrunk and petiole.

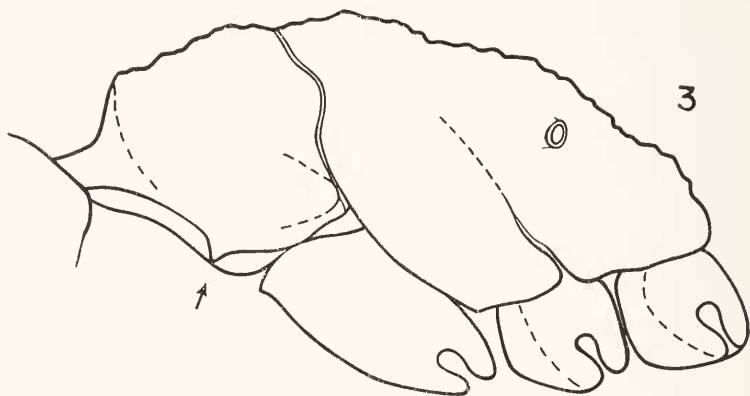


Figure 3. *Rhytidoponera laciniosa* Viehmeyer, worker, side view of alitrunk. Inferior pronotal tooth indicated by arrow.

3. Apical antennomere strongly bulbous, its length subequal to or $>$ the combined lengths of the second through penultimate funicular segments (Fig. 48); mandibles small, edentate (though frequently with a masticatory comb of short setae), largely or completely overhung by clypeus (Widespread in tropical and warm temperate regions)

Discothyrea Roger

Apical antennomere at most moderately enlarged, much shorter than combined lengths of second through penultimate funicular segments; mandibles larger, armed with 3 or more teeth or denticulae, not or only in very small part overhung by clypeus (Figs. 1, 23-35, 45, 46) (Wide-spread except S. America) *Proceratium* Roger

4. Inferior pronotal margins just in front of each anterior coxa with a distinct, usually acute tooth, best seen from an oblique dorsolateral view (Fig. 3) (rarely missing on one or both sides in individual specimens); posterior tarsal claws always with a distinct median tooth; posterior coxae unarmed above (Australia; N. Guinea, to N. Caledonia, s. Philippines)

Rhytidoponera Mayr

Inferior pronotal angles unarmed or forming an obtuse angle, or, in the rare cases where the angle is present and more nearly toothlike, then the posterior tarsal claws lack a median tooth, or else the posterior coxae are toothed above5.

5. Mesonotum rounded and prominent, surrounded by deeply impressed sutural lines; it and the propodeum forming distinct convexities separated by the deep transverse fissure of the metanotal remnant (Fig. 2); posterior coxae always unarmed (Neotropical) *Ectatomma* Fr. Smith Mesonotum and propodeum part of one continuous or near-continuous profile, interrupted at most by a suture-like groove at the position of the metanotum (rarely deep), or by an ill-defined impression in this region; posterior coxae armed above, or unarmed6.

6. Clypeus much modified, the median portion raised and produced as a short, blunt triangular point forward from the antennal insertions somewhat over the mandibles; antennal scrobes lateral, long and very deep (Russian Armenia, rare) *Aulacopone* Arnoldi Clypeus of normal form, broad and in one piece, not or only to a small extent covering the mandibles (Figs. 12, 41, 43, 44); antennal scrobes distinct and deep in only a few species7.

7. Dorsum of head without a median costa as distinct from other sculpture, or, if with a costa, it is short or not fully continuous (Figs. 41, 43, 44), and either the posterior coxae are toothed above (Figs. 17-20), or else the alitrunk and petiole are predominantly smooth and shining (Neotropical, Indo-Australian) *Gnamptogenys* Roger Dorsum of head with a distinct median costa from clypeus to vertex, continuous across frontal triangle (Fig. 12); posterior coxae unarmed above (Fig. 13); head and alitrunk thickly sculptured, usually hairy and pubescent and in large part opaque8.

8. Tarsal claws each with a prominent basal lobe and a large submedian tooth; propodeum with paired long teeth and petiole produced posteriorly as a single long spiniform tooth (Figs. 7-11); palpal formula

6, 4. (Neotropical) *Acanthoponera* Mayr
 Tarsal claws without prominent basal lobes, submedian tooth often absent, particularly on claws of posterior legs; propodeum and petiolar summit unarmed or with short teeth (Fig. 13); palpal formula 4, 3 or less (S. and C. America to Mexico; Australia, N. Zealand) .. *Heteroponera* Mayr

THE GENERA

ACANTHOPONERA MAYR

≡ *Ectatomma* subgenus *Acanthoponera* Mayr, 1862:732. Type: *Ectatomma* (*Acanthoponera*) *mucronatum* = *Ponera mucronata* Roger, 1860, by designation of Emery, 1911.

< *Acanthoponera*, Emery, 1911, p. 35; *nec* male.

= *Acanthoponera* subgenus *Acanthoponera*, Wheeler, 1932b:190.

It has already been shown (Brown, 1952c) that *Heteroponera* Mayr is the prior name for a group of species included by Emery in *Acanthoponera*, and ranked as subgenus *Anacanthoponera* by Wheeler (see below). *Heteroponera* deserves to be regarded as a separate genus on present evidence.

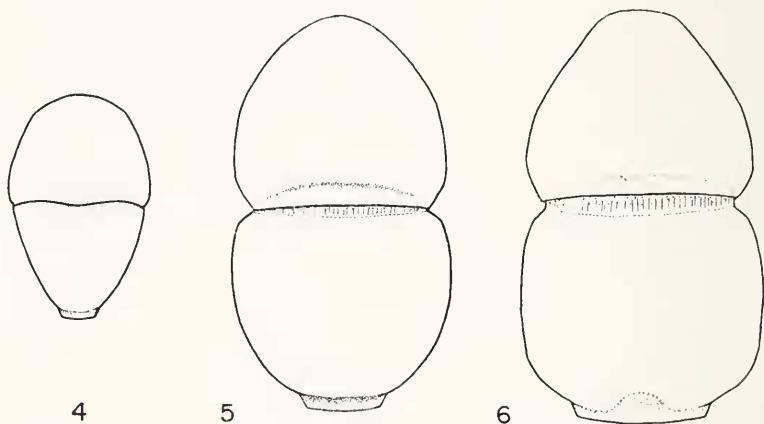
The species remaining in *Acanthoponera* as defined here are medium-sized ants (workers ranging from 5 to 10 mm. in outstretched length), generally of a yellowish or tan color, with large, convex eyes and shallow antennal scrobes. The propodeum bears a pair of teeth or spines (long and slender in worker), and the apex of the petiolar node is produced dorsocaudad as a slender subconical spine with a more or less acute tip. The tarsal claws are very well developed, and each has not only a strong submedian tooth, but also a prominent, narrow lobe resembling a third tooth. The palpi of the female and worker are segmented maxillary 6, labial 4 (this seems to be the formula in the single male available, although the basalmost segment in each of the palps of this specimen is not properly visible under the partly-retracted maxillae and labrum); this formula is the primitive one for the Formicidae, and it is not known to hold in any other ectatommine genus. The palpi are long and slender as compared to those of other ectatommines. The characters above are those expected of an epigaeic, nocturnal forager that climbs trees or other vegetation, habits now confirmed by observations of Weber (1939) and Wilson (personal communication) on *A. minor*.

The females of *Acanthoponera*, where known, are winged, slightly larger than workers from the same nest, and differ from the workers in the same ways that ponerines most often do. The female propodeal teeth are usually less well developed than in the worker. The color is the same or nearly the same as in the corresponding workers. The forewings have "complete" venation of the type of *Ectatomma*, but the hind wings differ from those of *Ectatomma* in that they lack the anal lobe. In the single *Acanthoponera* female available with wings, there is no trace of the first radial crossvein remaining, although such traces are present in the male specimen seen.

The male of this genus is known to me only from a single specimen sent by Father Borgmeier; I believe that this is the first true *Acanthoponera* male to be recorded. It will suffice here to describe this male as like a larger, more slender *Heteroponera* with tarsal claws as in worker-female *Acanthoponera*. A further notable character is the very extensive ventral excavation of the gaster; the cavity involves large parts of the second and following segments, and even the posteroventral border of the postpetiole. No such conformation exists in the few *Heteroponera* males I have seen, nor does it occur in other genera of ectatommines. More species must be examined in the male sex before we know whether or not this is a generic, or only a specific, character. The general color of this male is ferruginous yellow. The eyes are large, convex, and medially emarginate; the ocelli are large and clear. As already mentioned above, the male specimen seen has traces remaining of the first radial crossvein, visible in good light as tenuous veinlets extending downward from R toward Rs, but not reaching Rs before they fade out.

Acanthoponera is a rarely collected genus, less than a score of separate collections having reached myrmecologists to my knowledge. Nothing is known of its nesting habits or food, and the larva has never been seen, so far as I can learn. The genus is restricted to the New World, where it is known to range from Veracruz south into northwestern Argentina. Apparently it is restricted to forested country, although information on this is scanty. Probably an increase in night collecting in the tropics will give us more insight into the biology of this most interesting generalized ectatommine.

Eight names have been proposed for forms in the genus *Acanthoponera*, each based on one or two type specimens only. Material, whether determined or undetermined, is very scarce in collections, and the wide scattering of type depositions adds to the difficulty of revision at species level. Among the 21 worker and female specimens I have seen from 15 nests or individual collections, there appear to be only five distinct entities, each of which may represent a distinct species. It should be emphasized, however, that no real idea of species variability or species limits can be securely gained from such limited material. It is possible that all 21 specimens actually belong to one or two species only.



Figures 4-6. *Acanthoponera* spp., workers, dorsal views of first two gastric segments. Fig. 4, *A. minor*. Fig. 5, *A. mucronata*. Fig. 6, *A. peruviana* sp. nov., holotype. All drawn to same scale.

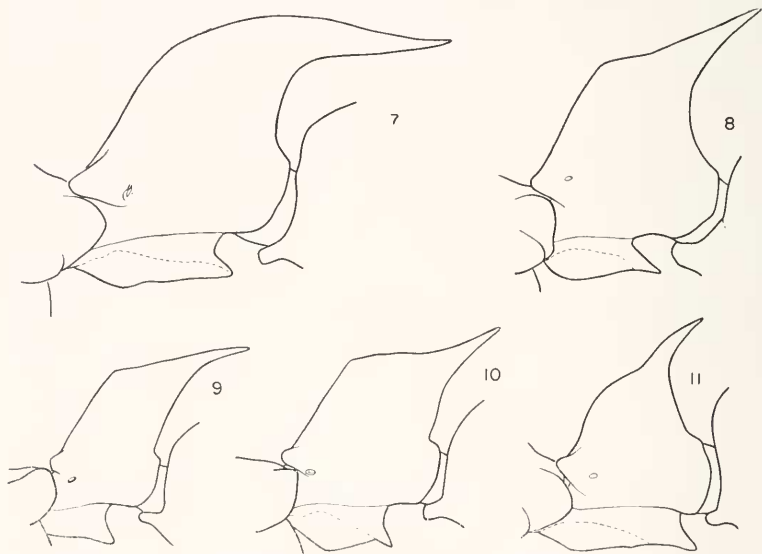
Of the five kinds, two have the “unconstricted” type of gaster, in which the second gastric segment is narrower than the post-petiole segment in which it is based, and from which it issues without notable constriction, tapering from this point toward the apex, as shown in Figure 4. Of the two kinds with unconstricted gaster, one averages a little smaller and has a petiole shaped as in Figure 9; to this kind belong the holotype of *schwarzi*, the cotypes of *spininodis*, and a specimen taken in Veraacruz by Wilson. The type of *spininodis* before me has the

head distinctly broader than in the Guatemalan or Mexican specimens, but the difference is not great enough to warrant continuing *spininodis* as a species apart from *minor*, which name I think should apply to the first unconstricted-gaster kind. In applying this name, I am relying on Forel's statement concerning the small size of *minor*, and also the fact that his type locality is Teapa, Tabasco, near the known localities for this species in Mexico and Guatemala from which my specimens have come. Forel also states that the spine of the petiolar node in *minor* is less strongly elevated and forms less of an angle with the node, which, if I interpret the statement correctly, applies well enough to the specimens here assigned to *minor*.

The second kind with unconstricted gaster is represented in my collection by a worker from Hamburg Farm, Santa Clara Prov., Costa Rica (F. Nevermann), and by three workers from 6 miles west of Santo Domingo de los Colorados, Pichincha, Ecuador (leg. E. I. Schlinger and E. S. Ross). The average size is a little larger than in *minor* (average head width, without eyes, ca. 1.04 mm., as against a head width of 1.00 mm. or less in *minor*), and the node is thicker from front to rear, with the spine elevated a bit more strongly (Fig. 10). The Costa Rican specimen is light yellowish ferruginous in color (teneral ?), and the Ecuadorian workers are considerably darker, yellowish-brown. The metanotal groove is represented by a distinct impressed line, averaging more distinct than in *minor*. I doubt whether these specimens belong to *minor*, and their correspondence with other described species seems doubtful also; perhaps they represent an undescribed species, and it seems best to describe and name them formally, in view of the probabilities, as *Acanthoponera crassa* sp. nov. [2].

Among the three kinds with constricted gaster, the smallest is represented by a single, winged female taken at Agudos, São Paulo State, Brazil (December 15, 1955), at light by W. W. Kempf. This specimen has a peculiarly-formed petiolar node (Fig 11), and the gastric dorsum is shining, with small, separated punctulae. The gastric constriction is distinct, but not especially strong. I cannot match this female with any known species, but it seems best to wait for material in which workers are associated before deciding whether it should be named.

Of the kinds with constricted gaster, one of intermediate-to-large size corresponds well to the types examined of *mucronata*, *wagneri* and *goyana* (Figs. 5, 8), and is undoubtedly the form described by Donisthorpe as *plaumanni*. This, the commonest form in collections, is known from Rio de Janeiro and Goias State in Brazil southward into northwestern Argentina and Bolivia. Through the kindness of Dr. G. Steinbach, of the Zoologisches Museum, Humboldt Universität, Berlin, I have been able to see



Figures 7-11. *Acanthoponera* spp., side views of petiolar node. Fig. 7, *A. peruviana* sp. nov., holotype worker. Fig. 8, *A. mucronata* worker from Beni R., Bolivia. Fig. 9, *A. minor* worker from Trinidad (syntype of *A. spinnodis* Weber). Fig. 10, *A. crassa* sp. nov., paratype worker from Ecuador. Fig. 11, *A.* sp. indet., female from Agudos, Sao Paulo, Brazil. All drawn to same scale.

Roger's *mucronata* type. Roger called the dorsa of postpetiole and succeeding segment, "dicht runzlig punktirt," which fits the next species discussed below better than it does this one. There is some size variation among different samples: *wagneri* type worker and three workers from Rurrenabaque, Beni, Bolivia (Mann leg.) average rather smaller (HW without eyes, 1.37-1.44

mm.) than those from the vicinity of Rio, where HW may reach 1.63 mm. in the worker. Cephalic indices are much the same in all of these samples, ranging from 90-94. Donisthorpe cited directly only larger size as a distinction for his *plaumanni*, but, although he stated that he had checked previous descriptions, it seems that he did not realize that there was no significant difference between his measurement and the one given originally by Roger. The *plaumanni* type is thus probably only an average specimen of *mucronata*.

The third kind of *Acanthoponera* with constricted gaster is near the previous kind (*mucronata*) in size; its HW without eyes is about 1.55 mm., and its cephalic index is similar (93), but its gaster is even broader and more depressed, particularly the second segment (Fig. 6). The second segment is also distinctive in having a semicircular impression extending from the impressed band along the posterior border forward into the raised portion of the tergite (Fig. 6). The petiole is of a particular conformation (Fig. 7), and the gastric dorsum is decidedly more coarsely, closely and irregularly punctured than in the preceding forms, perhaps conforming to Roger's "dieht runzlig punktirt," based, of course, on a female. We know that the female of *mucronata* has gastric punctation much like that of its worker, so the sculptural character is not just a caste or allometric difference. I have seen only a single worker of this last kind, from Tingo-Maria, Peru, but this is so distinct from the previously described species, including the closely related *mucronata*, that I have little hesitation in describing it as a new species, *A. peruviana* sp. nov. [1].

There is one named form of the genus that we have yet to consider: *A. goeldii* Forel. Dr. Wilson has examined the *A. goeldii* type and has compared it directly with *A. minor*. He feels that the two are different species, although their size is about the same. His quick sketch of the profile of alitrunk, petiole and gastric dorsum as seen from the side, and his description of the coarse sculpture and pilosity, particularly the rough, contiguous punctation of the gastric dorsum, are reminiscent of these features in *peruviana*, just discussed above, although the latter would of course be much larger than *goeldii*. At present, we know nothing directly of the size variation of either *peruviana*

or *goeldii*, but judging from the size variation known for *mucronata*, *minor* and *crassa*, it does not seem likely that *peruviana* and *goeldii* are large and small forms of one and the same species. The possible relationship of these two species should, however, be kept in mind in the future.

To summarize the present and provisional species-level taxonomy of *Acanthoponera*, we may recognize five reasonably distinct species at present named: *mucronata*, *peruviana*, *minor*, *crassa* and *goeldii*. A stray female seen cannot be referred with safety to any described species.

ACANTHOPONERA species

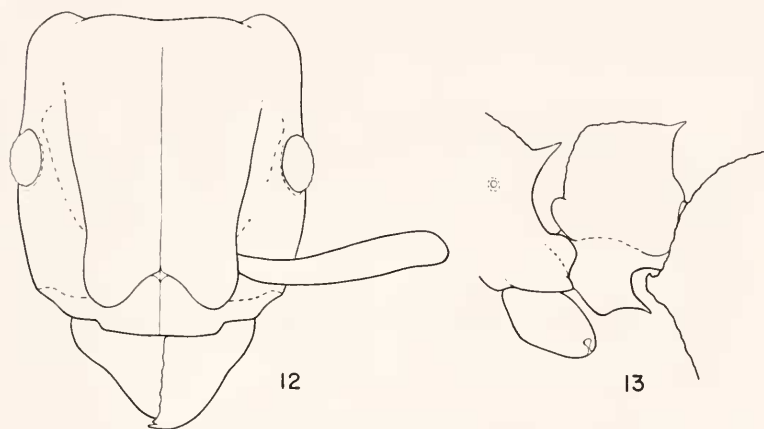
- (T) *crassa* Brown, sp. nov. C. America, Ecuador [2, Fig. 10]
- (T) *goeldii* Forel, 1912b:34. n. status c. Brazil
- (P) *minor* Forel, 1899a:9. n. status s. Mexico to Trinidad [2, Figs. 4, 9]
- (T) = *schwarzi* Wheeler, 1923b:188. n. syn.
- (T) = *spininodis* Weber, 1939:97. n. syn.
- (T) *mucronata* (Roger), 1860:299. s. Brazil, n. Argentina, Bolivia [1, Figs. 5, 8]
- (T) = *wagneri* Santschi, 1921:84. n. syn.
- (P) = *plaumanni* Donisthorpe, 1938:140. n. syn.
- (T) = *goyana* Borgmeier, 1939:418. n. syn.
- (T) *peruviana* Brown, sp. nov. e. Peru [1, Figs. 6, 7]

HETEROPONERA Mayr

- > *Heteroponera* Mayr, 1887:532. Type: *Heteroponera carinifrons* Mayr, 1887, monobasic.
- < *Acanthoponera* Mayr et auct.
- > *Paranomopone* Wheeler, 1915b:117. Type: *Paranomopone relictata* Wheeler 1915, monobasic. n. syn.
- > *Acanthoponera* subgenus *Anacanthoponera* Wheeler, 1923b:176. Type: *Ponera dolo* Roger, 1860, by original designation. Synonymy by Brown, 1952c.
- > *Heteroponera* (reinstated), Brown, 1952c.

See discussion of synonymy under *Acanthoponera*, above. Wheeler's *Paranomopone* was set up for the sole aberrant species *relictata*, segregated chiefly because of its well-marked scrobes and its angulate humeri. But other *Heteroponera* show lesser development of the scrobes, varying with the species, so that the difference is reduced to one of degree. Angulate humeri are found also in *H. leae*.

Essential characters of the workers are given in the generic key. Most known females of *Heteroponera* (*brouni*, *carinifrons*, *dolo*, *imbellis*, *relicta*) are wingless and ergatoid, but those of *dentinodis* and *schwebeli* have normal wings before nuptial flight. The few known males of *Heteroponera* have the usual gastric shape of other ectatommines, with no excavation beneath. The *relicta* worker palpi are segmented 4, 3; *brouni* and *imbellis* both have 3, 3 (my dissections); Kusnezov (1954) claims that the worker of *H. dolo* has 3, 2. In general, the species of the genus are small in size and form small colonies in soil, rotten wood or epiphyte masses. The distribution is discontinuous, with four species in Australia and New Zealand and six or seven in the New World tropics south into Chile.



Figures 12 and 13. *Heteroponera inca*, sp. nov., paratype worker. Fig. 12, full-face view of head. Fig. 13, side view of petiolar node and adjacent structures.

HETEROPONERA species

- (T) *brouni* (Forel), 1892:335. n. comb. N. Zealand: North I. [5]
- (T) = *kirki* (Wheeler), 1923b:184. n. syn.
- (P) *carinifrons* Mayr, 1887:533. Chile [3]
- (P) *dentinodis* (Mayr), 1887:541. n. comb. s. Brazil, Bolivia [3]
- (P) *dolo* (Roger), 1860:293. n. comb. se. Brazil to n. Argentina [3]
- (P) = *aurea* (Forel), 1913c:203. n. syn.
- (P) *imbellis* (Emery), 1895b:346. n. comb. sw. and e. Australia [4]

- (P) = *hilaris* (Forel), 1895:421. n. syn.
 (T) = *scabra* (Wheeler), 1923b:181. n. syn.
 (T) = *occidentalis* (Clark), 1926:47. n. syn.
 (P) = *nigra* (Clark), 1930:6. n. syn.
 (T) *inca* Brown, sp. nov. sw. Colombia [3, Figs. 12, 13]
 (?) *inermis* (Emery), 1894:143. n. comb. se. Brazil [3]
 (T) *leae* (Wheeler), 1923b:181. n. comb. N. S. Wales
 (T) *microps* Borgmeier, 1957:112. se. Brazil, Colombia [3]
 (?) *panamensis* (Forel), 1899a:9. n. comb. Panama [3]
 (T) *relicta* (Wheeler), 1915b:118. n. comb. n. Queensland
 (T) *schwebeli* (Luederwaldt), 1918:54. n. comb. se. Brazil [3]

Note: Among the new combinations, *relicta* is transferred from *Paranomopone*, and the rest from *Acanthoponera*. Santschi's *Acanthoponera* (*Anacanthoponera*) *reichenspergeri* is now put in *Gnamptogenys* [74]. *Heteroponera minuta* Kusnezov (1954:34) is a *nomen nudum* so far as I can determine at present.

*Key to known Australian-New Zealand
species of Heteroponera Mayr — workers*

1. Petiole tapering dorsally to an acute upwardly-directed tooth (e. N. S. Wales) *leae* (Wheeler)
 Petiole rounded or subtruncate above, without an acute tooth at the summit 2
2. Humeri angulate as seen from above; antennal scrobes distinct and deep, each surrounded by a fine, sharp carina and divided for much of its length by another (n. Queensland, rainforest) *relicta* (Wheeler)
 Humeri evenly and gently rounded as seen from above; antennal scrobes at most shallow, not distinctly bounded or divided 3
3. Petiolar node seen in lateral view profile fully erect, both anterior and posterior faces sloping very slightly inward toward the apical face, which is horizontal (e., s., sw. Australia) *imbellis* (Emery)
 Petiolar node seen in lateral view profile slightly inclined posteriad; the anterior nodal face sloping posteriad, apical face sloping upwards toward the rear; posterior face feebly concave, overhung by the posterodorsal angle, which projects slightly posteriad (N. Z.) *brouni* (Forel)

*Key to known New World species of
Heteroponera Mayr — workers*

1. Eyes minute, with only a very few facets; body size small, color ferruginous yellow, petiolar node thick scale-like, unarmed above (se. Brazil, Colombia) *microps* Borgmeier
 Eyes large, with many distinct facets 2

2. Full adult color black or dark piceous; petiolar node unarmed above (Chile) *carinifrons* Mayr
Full adult color testaceous to dark reddish-brown, but not black; petiolar node with or without a posterodorsal tooth-like process or angle 3.
3. Propodeal teeth well developed and acute, longer than half the distance between the centers of their bases and longer than broad at base; occipital angles each forming a prominent subtruncate lobe (best seen from side) (Figs. 12, 13); posterodorsal petiolar tooth present and acute; color deep reddish-brown. (sw. Colombia) *inca* sp. nov.
Propodeal teeth reduced or obsolete, never half as long as the distance between the centers of their bases 4.
4. Large ferruginous yellow species, HL 1.20 mm. or more, with well developed but blunt tooth on apex of petiolar node; small but distinct extra (submedian) teeth on all tarsal claws (se. Brazil to n. Argentina)
dolo (Roger)
Smaller species, HL 1.15 mm. or less; full adult color yellowish to reddish-brown; tarsal claws without distinct submedian teeth, at least on posterior legs 5.
5. Head relatively narrow ($CI < 85$); petiole in all sizes of workers terminating in a bluntly rounded posterodorsal border, without tooth or pointed process, petiolar node nearly or quite as long as high and as long as broad (se. Brazil) *schwebeli* (Luederwaldt)
Head broader ($CI > 85$); larger workers with a small, acute tooth on the posterodorsal petiolar border, this tooth vestigial in many smaller workers; petiolar node compressed from front to rear, distinctly higher than long and much broader than long (s. Brazil, Bolivia)
dentinodis (Mayr)

Judging from the original description, Emery's *inermis* would key to couplet 5, and it is probably the same as either *schwebeli* or *dentinodis*. It is possible, but perhaps not likely, that the large and small workers of *dentinodis* represent different species. [3] *H. panamensis* apparently runs to couplet 5, but we do not know enough about it to key it further.

RHYTIDOPONERA Mayr

≥ *Ectatomma* subgenus *Rhytidoponera* Mayr, 1862:731. Type: *Rhytidoponera araneoides* = *Ponera araneoides* Le Guillou, by designation of Emery, 1911.

- > *Rhytidoponera* subgenus *Chalcoponera* Emery, 1897a:548. Type: *Chalco-ponera metallica* = *Ponera metallica* Fred. Smith, by designation of Emery, 1911. Synonymy by Brown, 1953b:2.
- = *Rhytidoponera*, Emery, 1911:36-39, including subgenera *Rhytidoponera* + *Chalcoponera*. 1914:397.
- = *Rhytidoponera* + *Chalcoponera*, Wheeler, 1922:643-644. Clark, 1936:14-15. 1941:71.

This genus is distinguished by means of its dentiform inferior pronotal angles, each of which is situated, pointing downward, just in front of the fore coxa (Figure 3). These teeth are somewhat variable in shape, and at times their apices are blunt, but the sides are usually more or less concave, so that in basic form, the whole tooth is acute. Viehmeyer (1912) claims that the teeth are occasionally absent from some of his New Guinea examples, but it may be that he merely overlooked them in specimens that had the sternal plate of the prothorax in the dropped position, masking the silhouette. In such specimens, the tooth can be seen, with difficulty, only if the alitrunk is viewed from above and to one side, obliquely. Out of several thousand specimens of this genus, representing nearly all of the species from all over the range, I have seen only two specimens in which the inferior pronotal angles were absent or so reduced as to hardly deserve the term "tooth," and in one of the two cases this condition occurred on only one side of the insect. Clearly, absence of the pronotal teeth is an extremely rare occurrence of secondary nature, and perhaps represents a pathological condition.

Other characters of importance in generic diagnosis: well developed tooth present near midlength on all tarsal claws; posterior coxae unarmed above; promesonotal suture complete, apparently not ankylosed; eyes always present and well developed. Palpal segments, worker and female, appear to be constant at 3 maxillary, 2 labial, as based on dissections of several specimens each of *aurata*, *incisa*, *spoliata*, *taurus*, *impressa*, *metallica*. Males dissected (*impressa*, *mayri*) had 5 maxillary, 3 labial. The basal maxillary segment is very short in both sexes. Wing venation of both sexes as in *Ectatomma*, but anal lobe of hind wing absent.

A few species in related genera (e.g. *Heteroponera*) may bear a more or less angulate projection of the lower pronotal border corresponding to that of *Rhytidoponera*, but never so well marked as it usually is in the latter; furthermore, these species differ in one or more of the other characters, i.e., the posterior tarsal claws lack a distinct median tooth, or there is a tooth on the dorsal surface of the coxa, etc. In a few of the medium-sized and smaller species of *Rhytidoponera*, presumably closest to the generalized stock, normal winged males and females occur together in a proportion of nests in the same season at a given locality, and apparently nuptial flight and nest-founding occur much as in other generalized ponerines. In most species, however, true females become very scarce or absent, and their place is taken in whole or in part by fertile workers or by very worker-like ergatoids (Brown, 1953b; C. P. Haskins, *in litt.*); the males are produced over a wide season, which may in some cases last virtually the year around, and mating is accomplished when the males fly to another nest singly. Details of mating, reproduction and nest-founding in these forms remain to be clarified.

Larval morphology is discussed by the Wheelers (1952a: 124-127). Pupae are enclosed in rather dark-colored cocoons in the nests I have seen; the color approaches black in some arid-land Australian species. The male genitalia, at least in dissections of *R. impressa*, *R. metallica* and *R. mayri*, show only slight interspecific variation, and there appear to be no significant variations in these organs from the general plan as seen in other ectatommines. In particular, the volsella is very similar in outline to those of *Ectatomma* and the myrmicine genus *Myrmica*. The hypopygium shows differences in outline of the posterior border, but these are slight and in no case approach spectacular aberrations such as the forked member of *Paraponera* males.

Rhytidoponera ranges in Australia and adjacent islands, New Guinea, New Caledonia and neighboring parts of Melanesia in the east (but misses Fiji and New Zealand); westward it ranges to Timor, the Moluccas, and even to the southern Philippines (as based on a single series of the widespread form *araneoides*, collected by J. W. Chapman near Dumaguete, Negros Oriental). Considerable adaptive radiation has affected the genus, resulting

in around 100 known, validly-named species; the total will undoubtedly surpass 150 as collections become more complete. One large group of forms of increased size has taken up xeric niches in Australia (e.g., *mayri*, *punctata*), and has produced rain-forest-inhabiting species in Melanesia (e.g. *strigosa*, *laciniosa*); both of these ecological types tend to be dark, piceous or black in color. Members of the same group living in savannah or open-woodland areas of northern Australia are often reddish or ferruginous in color. Perhaps the most successful and abundant life-forms are represented by the smaller species of the *metallica* and *victoriae* groups, strongest in eastern and southern Australia. These are among the most plentiful and conspicuous of Australian ants in many localities, and they seem in many ways to take the place of general-feeding myrmecines, particularly *Myrmica*, in the northern countries; indeed, such species as the common greenhead ant, *R. metallica*, apparently play a role in the Australian environment that is relatively more important than that of the commonest of *Myrmica* species in most parts of the Northern Hemisphere. *R. metallica* and *R. victoriae* are common even in lawns and gardens in some Australian cities, and the former is respected for the potency of its sting, which produces a dull, lasting ache out of all proportion to the size of the insect.

There exists very little detailed information on foraging and feeding habits of this genus. The species vary greatly among themselves, and according to season, in diurnation of foraging. *R. metallica* is, in general, a predominantly daytime-foraging species, while *R. mayri* and other large deserticolous species forage mostly at night, at least during warm weather. Foraging is mostly limited to the ground and low plants, except in the rain-forest, where some species may normally live and forage in arboreal situations. Even in southern Australia, however, there are some species (*anceps*, *aspera*) that have been found running on tree trunks well above the ground, and perhaps most species do this to some extent. Food consists of insect remains, and probably in some cases honeydew is taken (Clark, 1936); what else, if anything, is gathered we do not know. Wilson will publish notes elsewhere on the foraging biology of the New Guinea species.

The nests of *Rhytidoponera* species are usually made in the soil, except in rain forest, where many species live in rotten logs, and a few even in the "peat" gathered in epiphytic masses on the trees. Soil nests may be with or without a stone or log as cover, and if without cover, a crater or masonry dome may be present or absent, according to species and habitat. Nests under stones are more frequent in cooler upland districts, and masonry domes with a very wide apical entrance (often "decorated" with pebbles or small lateritic concretions) are characteristic of some of the larger desert species. These desert nests are externally very similar to those built by certain arid-land *Camponotus* species.

The genus *Rhytidoponera* in the present broad sense has never been comprehensively revised, although Clark dealt with a majority of the larger Australian species in his review of 1936. Aside from its proposal of some fairly obvious synonymy, this work is largely unsatisfactory as a revision, the basic failure being a lack of proper emphasis on the constant differences separating species, where such differences exist. Apart from the inadequacies of this revision and of the material upon which it was based, however, the larger Australian species are particularly difficult taxonomically. Many of the entities (species or super-species) have vast, but strikingly discontinuous ranges, with more or less distinctly different populations completely isolated one from the next by great stretches of inhospitable country. The related questions of just how continuous this isolation is, and whether and to what extent such populations should be formally named, require much more study than Clark gave them, or than I can give them here.

Emery (1912) offered a brief review and key covering the smaller "Chalcoponera" species that is useful, but far out of date. Some revision of this group was completed by Brown (1954b), but basic revisionary work needs to be extended to the entire Australian fauna of the genus before a workable key will be possible.

Wilson [6], in his manuscript revision of the ants of Melanesia, has covered the *Rhytidoponera* species of that region and constructed a key to the species, so I shall for the most part avoid mention of Melanesian forms here. As a result of his cooperation during and after his trip to Melanesia and his subsequent tour of

the European museums, I am able to list new synonymy confirmed by him, some of which is drawn from his manuscript study. I have revised and keyed the New Caledonian species in this work [33].

At the time of his death in 1956, Clark had completed part of a manuscript dealing with the Australian *Rhytidoponera* and other ectatommines, but the status of this work at present is not clear. It is to be hoped that Australian and other interested specialists will soon be able to undertake a full revision of this difficult but very important continental fauna of the genus [8].

RHYTIDOPONERA species

Excluded from this list are names placed in synonymy by Clark (1936) and Brown (1954b); *Ponera ruginoda* Fr. Smith was placed in *Rhytidoponera* by Emery (1911), but is omitted here since the name was based on the male of *Myrmecia pilosula* Fr. Smith (Brown, 1953c).

- (T) *abdominalis* Viehmeyer, 1912:4. n. status. N. Guinea [6]
- (P) *acanthoponeroides* Viehmeyer, 1924:227. N. Caledonia [33]
- (P) *aciculata* (Fr. Smith), 1858:104. e. Australia [9, 20]
- (P) = *laevior* Stitz, 1911:352. n. syn.
- (T) *aenescens* Emery, 1900:312. N. Guinea [6]
- (T) *anceps* Emery, 1898:233. e. and sw. Australia [12]
- (T) *araneoides* (Le Guillou), 1842:317. Melanesia, etc. [6]
- (T) = *rugosa* (Fr. Smith), 1859:143. syn. Donisthorpe, 1932:454.
- (T) = *froggatti* Forel, 1910:10. n. syn. Wilson
- = *arcuata* Stitz, 1911:352. n. syn.
- (P) = *impressinodis* Stitz, 1912:498, n. syn. Wilson
- (P) = *ceramensis* Viehmeyer, 1914b:112. n. syn. Wilson
- (P) *aspera* (Roger), 1860:308. se. Australia [7]
- atropurpurea* Emery, 1914:396. ne. N. Caledonia [33]
- (P) *aurata* (Roger), 1861b:169. n. Australia
- (T) *barnardi* Clark, 1936:54. n. Queensland
- barretti* Clark, 1941:81. e. Australia
- (P) *borealis* Crawley, 1918:88. n. status. Australia: Darwin dist. [11, 28]
- (P) = *brunnea* (Clark), 1941:86, n. syn.
- (T) *carinata* Clark, 1936:54.
- (T) *celtinodis* Wilson, ms. sp. nov. N. Guinea [6]
- (T) *cerastes* Crawley, 1925:584. nw. Australia
- (P) *chalybaea* Emery, 1901:51. se. Australia [7]
- (T) *chnoopyx* Brown, sp. nov. n. Queensland [16]

- (T) *clarki* Donisthorpe, 1943:115, nom. pro *hilli* (Clark) Queensland [32]
- (P) = *obscura* Forel, 1900b:60, nec Emery, 1896. n. syn.
- (T) = *hilli* (Clark), 1941:85, nec Crawley, 1915. n. syn.
- (T) *convexa* (Mayr), 1876:92. e. Australia [13, 19]
- (P) *cornuta* Emery, 1895b:347. n. Queensland
- (P) *crassinodis* Forel, 1907:270. W. and e. Australia
- (P) *cristata* (Mayr), 1876:91. N. S. Wales, s. Queensland
- (P) *croesus* Emery, 1901:50. e. N. S. Wales, se. Queensland [7]
- (T) *douglasi* Brown, 1952b:137, nom. pro *levior* Crawley sw. Australia [17]
- lubia* Crawley, 1915:132. Australia: Darwin dist.
- (T) *cremita* Clark, 1936:78. e. Australia
- (T) *ferruginea* Clark, 1936:48. nw. Queensland
- flavicornis* Clark, 1936:64. W. Australia
- flavipes* (Clark), 1941:84. S. Australia
- (?) *findersi* Clark, 1936:60. S. Australia [17]
- (T) *foreli* Crawley, 1918:87. Australia: Darwin dist.
- (T) *foveolata* Crawley, 1925:581. sw. Australia
- (T) *fulgens* (Emery), 1883:148. N. Caledonia [33]
- (T) = *socrula* Emery, 1914:395. n. syn.
- fuliginosa* Clark, 1936:47. ne. S. Australia
- greavesi* Clark, 1941:81. n. Queensland
- gregoryi* Clark, 1936:47. ne. S. Australia
- (T) *haeckeli* Forel, 1910:15. Queensland: C. York [30]
- hanieli* Forel, 1913b:660. Timor
- (T) *hilli* Crawley, 1915:131. Australia: Darwin dist. [18, 32]
- (P) *impressa* (Mayr), 1876:92. e. Queensland [7]
- (P) *incisa* Crawley, 1915:132. e. Australia [17]
- (P) *inops* Emery, 1900:312. N. Guinea [6]
- (T) = *striata* Donisthorpe, 1949b:744. n. syn. Wilson
- (P) *inornata* Crawley, 1922:436. n. status sw. Australia [14]
- (T) = *carbonaria* Wheeler, 1934:139. n. syn.
- (T) *kurandensis* Brown, sp. nov. n. Queensland [15]
- (T) *laciniosa* Viehmeyer, 1912:5. N. Guinea [6, Fig. 3]
- (P) = *petiolata* Viehmeyer, 1912:5. n. syn. Wilson
- (T) *lamellinodis* Santschi, 1919b:327. n. Queensland [30]
- laticeps* Forel, 1915b:12. n. Queensland [25]
- (T) *maledicta* Forel, 1915b:15. n. status n. Queensland [21, 31]
- (T) *maniae* Forel, 1900b:57. S. Australia, w. N. S. Wales [18, 19]
- (T) = *spatiata* Forel, 1900b:58. n. syn.
- (T) *mayri* (Emery), 1883:150. arid s. half of Australia [20]
- (P) = *glabrior* Forel, 1907:268. n. syn.
- (P) = *quadriceps* Clark, 1936:30. n. syn.
- (T) = *stridulator* Clark, 1936:37. n. syn.

- (P) = *occidentalis* Clark, 1936:39. n. syn.
 (P) = *petiolata* Clark, 1936:41, nec Viehmeyer, 1912, n. syn.
 (P) = *dixonii* Clark, 1936:46. n. syn.
 (T) *metallica* (Fr. Smith), 1858:94. Australia, except far n. [14, 21]
 (T) = *purpurascens* Wheeler, 1915c:805. n. syn.
 (T) = *varians* Crawley, 1922:436. n. syn.
 (T) = *cacciliae* Viehmeyer, 1924:227. n. syn.
 = *pulchra* (Clark), 1941:86. n. syn.
 (T) *micans* Clark, 1936:62. W. Australia
 (T) *mirabilis* Clark, 1936:29. e. Australia [20]
 (T) *nexa* Stitz, 1912:500. n. status N. Guinea [6]
 (T) = *major* Stitz, 1912:501. n. syn. Wilson
 = *gagates* Donisthorpe, 1941:51. n. syn. Wilson
 (T) = *waigeuensis* Donisthorpe, 1942:703. n. syn. Wilson
 (?) *nigra* Clark, 1936:81. S. Australia [19]
 (T) *nitida* Clark, 1936:45. w. N. S. Wales
 (T) *nodifera* Emery, 1895b:348. e. N. S. Wales, se. Queensland
 (P) *nudata* (Mayr), 1876:91. Queensland
 (T) *numeensis* E. André, 1889:221. N. Caledonia [33]
 (T) = *acupuncta* Emery, 1914:396. n. syn.
 (T) *peninsularis* Brown, sp. nov. C. York Peninsula [27]
 (T) *pilosula* Clark, 1936:80. w. N. S. Wales
 (T) *pulchella* (Emery), 1883:149. N. Caledonia [33]
 punctata (Fr. Smith), 1858:104. S. (and W.?) Australia [17]
 (T) *punctigera* Crawley, 1925:582. sw. Australia
 (?) *punctiventris* Forel, 1900b:56. n. status N. S. Wales
 (P) *purpurea* (Emery), 1887:444. N. Guinea, n. Queensland [6, 7]
 (P) *reflexa* Clark, 1936:76. Australia: Darwin dist. [22]
 (P) *reticulata* Forel, 1893:458. Australia: Darwin dist. [23]
 (P) *rotundiceps* Viehmeyer, 1914a:28. n. N. Guinea [6]
 (P) *rufescens* Forel, 1900b:58. n. status e. Queensland [13]
 rufithorax Clark, 1941:82. n. Australia
 (P) *rufiventris* Forel, 1915b:11. n. and W. Australia [24]
 (T) *rufonigra* Clark, 1936:58. sw. Australia [17]
 (P) *scaberrima* Emery, 1895b:347. n. Queensland [10]
 (T) = *malandensis* Forel, 1915b:10. n. syn.
 (T) *scabra* (Mayr), 1876:90. e. Queensland [25]
 socrus Forel, 1894:236. w. N. S. Wales
 (T) *spoliata* Emery, 1895b:348. n. Queensland [25]
 (T) *strigosa* Emery, 1887:444. n. status N. Guinea, etc. [6]
 (T) = *intricata* Emery, 1910:533. n. syn. Wilson
 (T) = *curvata* Stitz, 1912:499. n. syn. Wilson
 = *schlaginhaufeni* Viehmeyer, 1912:4. n. syn. Wilson

- (T) = *nitens* Donisthorpe, 1949e:403. n. syn. Wilson
 (T) *subcyanca* Emery, 1897a:548. N. Guinea, etc. [6]
 (T) = *transversiruga* Emery, 1910:532. n. syn. Wilson
 (P) = *aruana* Karawajew, 1925:78. n. syn. Wilson
 (P) = *wallacei* Donisthorpe, 1932:474. n. syn. Wilson
 (T) *tasmaniensis* Emery, 1898:232. n. status se. Australia [21]
 (T) = *cristulata* Forel, 1900b:59, n. syn.
 (P) *taurus* Forel, 1910:12. n. and c. Australia [20, 28]
 (T) *tenuis* Forel, 1900b:58. coastal n. Queensland [27]
 (T) *trachypyx* Brown, sp. nov. Australia: c. N. Territory [28]
 (T) *turneri* Forel, 1910:14. Queensland: C. York [30]
 (T) *tyloxyis* Brown and Douglas, sp. nov. W. Australia [29, Figs. 36, 37]
 (T) *versicolor* Brown, sp. nov. mts. of N. Caledonia [33]
 (T) *victoriae* E. André, 1896:261. e. Australia [15, 31]
 (T) = *modesta* Emery, 1895b:348. n. syn.
 (T) = *scrobiculata* Forel, 1900b:59. n. syn.
 (T) = *ccldarensis* Forel, 1915b:15. n. syn.
 (T) *violacea* Forel, 1907:269. n. status W. Australia [13]
 (T) = *opacior* Crawley, 1925:583. n. syn.
 (P) *viridis* (Clark), 1941:83. ne. S. Australia [26]
 (T) *wilsoni* Brown, sp. nov. N. Caledonia [33]
yorkensis Forel, 1915b:12. Queensland: C. York

PARAPONERA Fr. Smith

- = *Paraponera* Fr. Smith, 1858:110. Type: *Paraponera clavata* = *Formica clavata* Fabricius, monobasic.
 = *Paraponera*, Emery, 1911:27.

This monotypic genus, exclusively neotropical, is well known and easily recognized from its giant size. Smith correctly noted the palpal segmentation: all castes of both sexes have a 5,3 formula. The female is winged, and both it and the worker have the hypopygium bordered on each side by an upwardly-directed comb of slender spinules. The male subgenital plate is in the form of a slender, upcurved biramous fork resembling that seen in the males of cerapachyines. The hind wings of both sexes have a well-developed anal lobe. Weber (1946) has discussed certain aspects of the morphology and habits, and has called attention to the resemblances *Paraponera* bears to *Ectatomma*. Larval morphology is covered by G. C. and J. Wheeler (1952a:117, pl. 2, figs. 1-9).

AULACOPONE Arnoldi

= *Aulacopone* Arnoldi, 1930a:139. Type: *Aulacopone relicta* Arnoldi, 1930a:140, figs. 1-5, female, monobasic.

All that is known to me about the remarkable species *A. relicta* is contained in the original description, based on a single dealate female — still the sole specimen known. The genus, if correctly described and figured, is apparently closest to *Heteroponera*, but differs widely in the structure of the fronto-clypeal area (see key to genera, above). The type locality is in intermediate mountain forest at Alazapin, 40 km. southwest of Lenkoran in Russian Armenia.

ECTATOMMA Fr. Smith

< *Ectatomma* Fr. Smith, 1858:102. Type: *Ectatomma tuberculatum* = *Formica tuberculata* Olivier, by designation of Bingham, 1903.

= *Ectatomma* subgenus *Ectatomma*, Emery, 1911:42.

= *Ectatomma* subgenus *Ectatomma*, Wheeler, 1922:643.

In the Emery-Wheeler classification, *Ectatomma* included the nominate and three other subgenera: *Gnamptogenys*, *Poneracantha*, and *Parectatomma*. Mann (1922) and Borgmeier (1929) proposed the elevation of *Gnamptogenys* to generic rank. Santschi followed Emery and Wheeler, and even added two more subgenera in 1929, each subgenus to include a single species. These two names, *Tammoteca* and *Commateta*, never gained wide acceptance, and it seems clear that both should be placed in the synonymy of *Gnamptogenys* (see below). When all the species placed under *Ectatomma* in the sense of Emery and Wheeler are assembled, one finds that the assemblage is divided into two distinct groups on the basis of both adults and larvae. Concerning the larvae, the Wheelers (1952b) say, "*Emeryella*, *Stictoponera*, *Ectatomma* (*Poneracantha*), *E.* (*Parectatomma*), *E.* (*Gnamptogenys*) are so similar that they can be separated only by differences of a sort that distinguish species elsewhere. It is interesting to note that Emery in the *Genera Insectorum* regarded *Emeryella* as very close to *Gnamptogenys*." The Wheelers regard *Ectatomma sensu stricto* larvae as quite different from those of the genera and subgenera just listed (1952b: 657, 658).

My own studies, based on adult characters, are in good agreement with the larval findings. I find several good differences separating *Ectatomma* from its erstwhile sister subgenera, and when one gets used to the idea of separation, it is even a bit surprising that these two groups of species have been associated in one genus for so long. The workers of the true *Ectatomma* resemble in some ways those of the larger species of *Rhytidoponera* from Australia and New Guinea, and like *Rhytidoponera*, they always lack a tooth on the dorsal surface of the posterior coxa. The build of the worker alitrunk is distinctive, with its convex mesonotum (Fig. 2) set off on all sides by distinct sutural grooves, and its tendency (damped in two or three species) to develop three eminences on the pronotum; also, several of the species have evolved slit-shaped propodeal spiracles. The antennal insertions are covered by translucent bullae, very prominent and situated just within the frontal lobes, and the petiolar node is erect and more or less angular in the worker and female. The sexes have a well developed anal lobe on the hind wing, a character shared with *Paraponera*. All tarsal claws preserve the distinct submedian tooth.

Male genitalia are much like those of *Paraponera* (Weber, 1946), but the hypopygium is of the normal form. The wing venation of both sexes is of the "complete" type, the forewing having all of the primitive formicid elements except the first radial crossvein. The palpi are segmented 2, 2, in worker and female; the basal segment of the maxillary palp is broadened and strongly compressed, but is not very short like those of *Gnamptogenys* and *Rhytidoponera*. The apical segment of the maxillary palp is slender. In the male, the maxillary palp is normally 5-segmented, but occasionally the terminal segment is very short and fused to the preceding segment, so that there are only four movable segments. Relative lengths of segments variable, especially the last two. Male labial palpi 3-segmented.

The species of *Ectatomma* are mostly widespread and relatively successful insects, frequently common over wide areas of Mexico and Central and South America, southward into northern Argentina. Some species (*quadridens*, *ruidum*) are more usually encountered in forested areas, while others may occur in more open, even in arid areas (*opaciventre*). *E. tuberculatum* is

found in rather arid districts as well as in rain forest. The genus is, however, rather strictly confined to those parts of the Americas with a tropical or warm subtropical climate. The biology of two of the common species (*tuberculatum* and *ruidum*) is reviewed in a full and informative account by Weber (1946). Among his more interesting observations, one may note that both he and Cook found that the eggs laid by the females became very dark in color, whereas worker-laid eggs may in some cases remain light in color, as is usual for other ants; also, the larvae are capable of some limited locomotion by crawling.

The species-level taxonomy of *Ectatomma* has been more or less confused, partly by mixups involving *muticum* and *edentatum*, also *ruidum* and *morgani*, and partly because of excessive accumulation of infraspecific names. Most of this confusion is rather simply dissipated when sufficient material of all the variable species is considered at one time. However, there remain a number of problems that can be settled only when more material from critical areas reaches the proper collections. Outstanding among these problems are the status of *confine* and *aztecum*, and the two north-south species pairs in South America, *lugens-permagnum* and *edentatum-morgani*. Weber (*op. cit.*) has already suggested synonymy for the variants of *E. tuberculatum*, and his suggestions are mostly formally adopted here.

ECTATOMMA species

- (P) *acrista* Forel, 1909:254. n. status. Paraguay [42]
- (T) *aztecum* Emery, 1901:50. s.w. Mexico [34]
- (?) *confine* Mayr, 1870a:397. "New Granada;" C. America? [35, Fig. 2]
- (P) *edentatum* Roger, 1863:173. s. Brazil, n. Argentina [36, 41]
- (P) = *iris* Forel, 1909:253. n. syn.
- (P) = *densestriata* Forel, 1912b:31. n. syn.
- (P) = *inversa* Santschi, 1912b:521. n. syn.
- (T) *lugens* Emery, 1894:144. n. status. Amazon-Orinoco basins [37]
- (?) *macdonaghi* Forel, 1915a:351. n. status. n. Argentina [36]
- (P) *morgani* Forel, 1912b:31. Amazon-Orinoco basins [38]
- (P) *muticum* Mayr, 1870b:962. n.e. Brazil: Ceara, etc.; Mexico? [41]
- (P) = *lobulifera* Forel, 1909:254. n. syn.
- (P) *opaciventris* Roger, 1861b:169. s. Brazil, n. Argentina [39]
- (P) = *concolor* Santschi, 1919a:37. n. syn.
- (T) *permagnum* Forel, 1908:342. n. status. e. Brazil to Bolivia and n. Argentina [37]

- (P) = *strigosum* Emery, 1894:144, nec Emery, 1887. n. syn.
 (P) = *confusa* Forel, 1909:266. n. syn.
 (P) = *acrea* Forel, 1912b:32. n. syn.
 (T) *planidens* Borgmeier, 1939:418. s. Brazil [40]
 (P) *quadridens* (Fabricius), 1793:362. Panama to n. Argentina [40]
 (P) *ruidum* Roger, 1860:306. s. Mexico to Amazon Basin [34, 38]
 (P) *tuberculatum* (Olivier), 1791:498. Mexico to n. Argentina [42]
 (P) = *punctigerum* Emery, 1890b:56. syn. after Weber, 1946.
 (P) = *irregularis* Santschi, 1921:83. syn. after Weber, 1946.

A key to the species of Ectatomma, based primarily on the workers

Note: The postpetiole and first gastric segment are one and the same. Both first and second gastric segments usually bear coarse piligerous punctures in addition to the sculpture discussed in this key. See qualifications marked with an asterisk (*) at end of key.

1. Second gastric segment very finely, superficially and evenly punctulo-reticulate and opaque, the reticulation not forming striolae except possibly some very fine indistinct ones near the margins or sides, away from the center of the disc 2
 Second gastric segment in large part distinctly striate or striolate over the center of the disc 3
2. Fine punctulo-reticulation of first gastric segment unrelieved on the disc (but often forming fine striolation across vertical anterior face of the tergite) (n. Argentina, s. Brazil) *opaciventre* Roger
 Fine sculpture of first gastric segment generally overlain loosely by fine, irregular rugulation, transversely arched in front (Amazon Basin to Venezuela) *lugens* Emery*
3. First and second gastric segments, as well as head, alitrunk and petiole, very regularly and evenly striate, similarly finely throughout 4
 The second gastric segment, and often also the posterior part of the first, with sculpture finer or otherwise contrasted to that of the anterior half of the first segment 5
4. Individual costulae of sculpture all with rather smooth and even surfaces; color of full adults approaching black (Venezuela to n. Argentina and Bolivia) *quadridens* (Fabricius)
 Individual costulae of sculpture on head and alitrunk, especially on the

- pronotum, with eroded, rough surfaces, in extreme manifestation yielding a beaded effect at magnifications of 80X or more; usual full adult color dull yellowish-brown, with alitrunk and gaster patchily infuscated above (se Brazil) *planidens* Borgmeier
5. Eye moderate in size, its greatest diameter approximately equal to, or shorter than, the length of the apical antennal segment 6
 Eye larger, its greatest diameter distinctly greater than the length of the apical antennal segment 8
6. Pronotum with an obtuse, but very high and prominent median eminence and small but distinct, subrectangular lateral (humeral) tubercles Fig. 2) (Colombia, C. America, rare) *confine* Mayr
 Pronotum without, or with only a very indistinctly differentiated median eminence; lateral tubercles or angles obsolete 7
7. Full adult color ferruginous brown, with yellowish legs and antennae; sculpture rather coarse and irregular, wavy or vermiculate on first gastric segment (Peru to Trinidad; see text) *morgani* Forel*
 Full adult color piceous to black, legs and antennae not or scarcely lighter; transversely arched striation of anterior dorsum of first gastric segment rather smooth and regular, not wavy (s. Brazil, n. Argentina) *edentatum* Roger*
8. Node of petiole seen from side high, narrow, distinctly constricted near the middle of its height; anterior half of first gastric segment coarsely vermiculate or ruggedly reticulate-rugose (e. Mexico to Trinidad and Ecuador) *ruidum* Roger
 Node of petiole seen from side gradually increasing in thickness from apex to base; at least the anterior half of the first gastric segment with rather regular, parallel rugulation or costation, this not or only gently wavy 9
9. Median and lateral eminences of pronotum suppressed, usually quite obsolete, or the laterals represented by brief indistinct dorsolateral margination; second gastric segment superficially transversely striate, the striation spaced and partly effaced anteriorly, so that this much of the disc is distinctly shining (Ceara, etc., in ne Brazil; ?sw Mexico) *muticum* Mayr
 Median and (more particularly) lateral pronotal eminences developed as more or less salient eminences or angles; second gastric segment finely, densely and regularly striolate (except in some samples of *tuberculatum*, but in these, the lateral pronotal eminences are very well developed and acute) 10

10. All surfaces of body and appendages covered with very numerous short, erect hairs; in perfect full-face view, more than 15 erect hairs projecting beyond the straight outline of the cheek between eye and anterior corner of head (sw Mexico) *aztecum* Emery
Erect hairs present, but longer and much less abundant; in perfect full-face view, fewer than 10 hairs (often none at all) visibly projecting beyond the straight outline of the cheek between eye and anterior corner of head 11
11. In perfect full-face view, the occipital border straight to feebly convex, usually with more or less rectangular occipital angles; head coarsely reticulate-rugose, the rugae enclosing foveae with more or less shining bottoms; color ferruginous except in N. South America, where some populations are more brownish (Mexico to n. Argentina)
tuberculatum (Olivier)*
In perfect full-face view, the occipital border broadly concave; occipital angles narrowly rounded; head finely longitudinally striate, with some V-like rugules across the vertex; color deep reddish to black (e. Brazil to n. Argentina and Bolivia) *permagnum* Forel*

*The form *acrista* Forel, from Paraguay and vicinity, is probably only a southern extreme geographic variant of *tuberculatum* and is not keyed. The species pairs *lugens-permagna* and *edentatum-morgani* may indicate merely the ends of respective clines of single species. In both cases, material from the crucial intermediate zone in the Amazon Basin is lacking or insufficient.

GNAMPTOGENYS Roger

- > *Gnamptogenys* Roger, 1863:174. Type: *Ectatomma* (*Gnamptogenys*) *tornatum* = *Ponera tornata* Roger, 1861, by designation of Emery, 1911.
- > *Ectatomma* subgenus *Stictoponera* Mayr, 1887:539. Type: *Ectatomma corale* Roger, 1860, by designation of Bingham, 1903. n. syn.
- > *Ectatomma* subgenus *Holcoponera* Mayr, 1887:540. Type: *Holcoponera striatula* = *Gnamptogenys striatula* Mayr, 1883, by designation of Emery, 1911. n. syn.
- > *Alfaria* Emery, 1896:41. Type: *Alfaria simulans* Emery, 1896, monobasic. n. syn.
- > *Ectatomma* subgenus *Poneracantha* Emery, 1897a:547. Type: *Ectatomma* (*Poneracantha*) *bispinosum* = *Ectatomma* (*Holcoponera*?) *bispinosum* Emery, 1890, monobasic. n. syn.
- > *Rhopalopone* Emery, 1897a:549. Type: *Rhopalopone epinotalis* Emery, 1897, monobasic. n. syn.
- > *Emeryella* Forel, 1901a:334. Type: *Emeryella schmitti* Forel, 1901, monobasic. n. syn.

- > *Ectatomma* subgenus *Mictoponera* Forel, 1901a:372. Type: *Ectatomma* (*Mictoponera*) *diehli* Forel, 1901, monobasic. syn. Emery, 1911.
- > *Ectatomma* subgenus *Parectatomma* Emery, 1911:44. Type: *Ectatomma triangulare* = *Ectatomma* (*Gnamptogenys*) *triangulare* Mayr, 1887, by original designation. n. syn.
- > *Spaniopone* Wheeler and Mann, 1914:11. Type: *Spaniopone haytiana* Wheeler and Mann, 1914, monobasic. n. syn.
- > *Wheeleripone* Mann, 1919:282. Type: *Wheeleripone albielava* Mann, 1919, by original designation. n. syn.
- > *Opisthosecyphus* Mann, 1922:4. Type: *Opisthosecyphus scabrosus* Mann, 1922, monobasic. n. syn.
- > *Ectatomma* subgenus *Commata* Santschi, 1929c:476. Type: *Ectatomma* (*Parectatomma*) *bruchii* Santschi, 1922, by original designation, monobasic. n. syn.
- > *Ectatomma* subgenus *Tammotoca* Santschi, 1929c:476. Type: *Ectatomma concinnum* = *Ectatomma concinna* Fred. Smith, 1858, by original designation, monobasic. n. syn.
- > *Emeryella* subgenus *Barbourella* Wheeler, 1930:10. Type: *Emeryella* (*Barbourella*) *banksi* Wheeler, 1930, by original designation, monobasic. n. syn.

The genera and subgenera here placed in synonymy have been the subjects of long and painstaking inquiry. It was clear from the beginning of the study that the old association of *Gnamptogenys* with *Ectatomma* (q.v.) within one genus was incorrect, as Mann (1922) and Borgmeier (1929) already had indicated by their use of *Gnamptogenys* as a separate generic name. It now seems clear that *Ectatomma* (*sensu stricto*) is a phyletically "lower" ectatommine genus, whereas *Gnamptogenys* and the synonyms listed above constitute the "upper" ectatommines. As the present study progressed, the "upper" genera fell into four groups, as follows:

GNAMPTOGENYS Group (New World)

Gnamptogenys, *Poncracantha*, *Emeryella*, *Parectatomma*, *Commata*, *Tammotoca*, *Barbourella*.

HOLCOPONERA Group (New World)

Holcoponera, *Spaniopone*.

STICTOPONERA Group (Old World)

Stictoponera, *Rhopalopone*, *Mictoponera*, *Wheeleripone*.

ALFARIA Group (New World)

Alfaria, *Opisthoscyphus*.

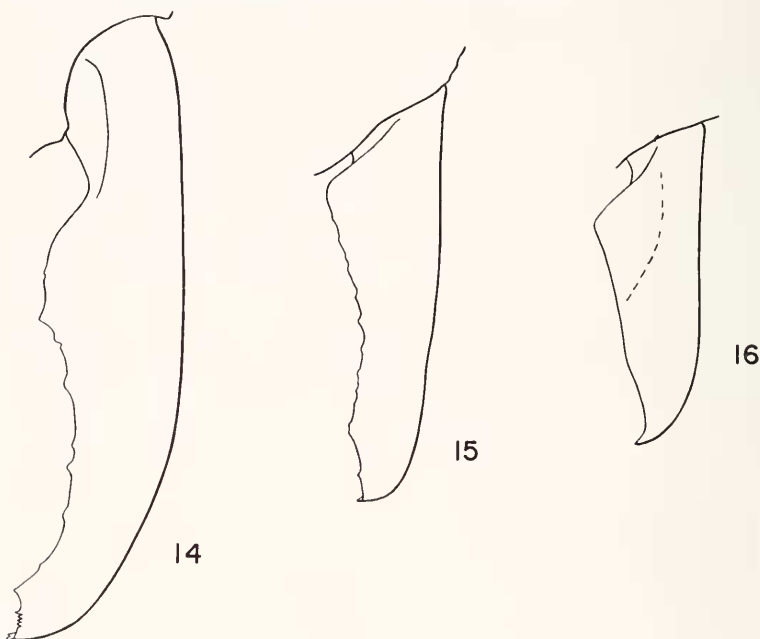
Within each group, it is now safe to consider the genera synonymous. The justification for this synonymy is now offered for each group in turn.

GNAMPTOGENYS Group

The genera and subgenera in this group have been separated primarily on the basis of mandibular structure, and secondarily on alitruncal suturation, plus propodeal armament. The mandibular forms represented grade through from the extremes by way of a remarkably finely stepped array of intermediate species, assembled for the first time during the course of this study. This series of species can be divided only by the drawing of arbitrary lines, with no natural gaps to help in the drawing of these lines. The other characters that have been used to divide this assemblage of species prove useless because they are not in concordance with the more conspicuous mandibular tendencies. Of course, it is possible to eliminate the troublesome "intermediate" species, those carrying "diagnostic" characters discordantly, by relegating them to monotypic subgenera, as Santschi did with *Tammotecca* and *Commateta*. But Santschi's approach, whether cynical or extremely naive, seems justly to have been shunned by other specialists in the Formicidae.

Everything considered, it makes better biological sense to drop the artificial generic assortment of these species. This done, it becomes easier to recognize and describe the very interesting phylogenetic trends in development of the mandibles within the group, considered as one radiating unit. The primitive mandibular form apparently is the triangular type more or less characteristic of the *Paracetatomma* species, and also found more or less faithfully copied in *Poneracantha* and in the species of the *Holcoponera*, *Stictoponera*, and *Alfaria* groups. In this type, apical and basal borders are approximately perpendicular to one another (Figs. 41, 43, 44), but, contrary to the impression given by some older writings, these two borders most often meet through a distinct curve, even considering that this curve can in some cases be rather sharply rounded.

In the *Gnamptogenys* group, variation away from the triangular condition follows a double morphocline (*sensu* Maslin 1952). One of the two series of variants, expressed approximately in the consecutive arrangement *aculeaticorae* → *hartmani* → *nigrifrons* → *bruchii* → *haenschi* → *concinna* → *alfaroi* → *tornata* → *mordax*, shows a tendency toward broadening the curve of the basal angle until, in extreme cases such as *mordax*,



Figures 14-16. *Gnamptogenys* spp., dorsal views of left mandibles. Fig. 14, *G. semiferox*, sp. nov., paratype worker. Fig. 15, *G. mediatrix* sp. nov., holotype worker. Fig. 16, *G. rastrata* (Mayr), holotype female. All drawn to same scale.

the basal and apical borders have become continuous, and the mandible has achieved a linear shape. Accompanying this change of shape, the blade of the mandible is becoming more and strongly deflected ventrad in its apical half, so that the mandibles as seen from the side are strongly arched, while the dentition transforms into a vaguely double-ranked set of blunt tubercles.

If we follow the other morphocline outward from *aculeaticoxae* in the series represented roughly by *aculeaticoxae* \rightarrow *triangularis* \rightarrow *rastrata* \rightarrow *mediatrix* \rightarrow *semiferox* \rightarrow *Emeryella schmitti*, we see the blade first lengthen without losing its triangular shape, and then, beginning with *rastrata* and *mediatrix*, it becomes concave along the masticatory margin and more convex along the outer margin, with further increase in length (Figs. 14-16), until an extreme falciform shape is attained in *schmitti*. The mandible of *E. (Barbourella) banksi* belongs with the group just discussed, but it is slightly aberrant in its own right; the difference is not great enough to support the separation of *banksi* in a monotypic genus or subgenus. The morphocline that obliterates the distinction between *Gnamptogenys* and *Emeryella* as genera also brings *Barbourella* into the fold. It should be noted that this morphocline has been completed by the two new species described in this contribution — *G. mediatrix* and *G. semiferox* [78, 77].

The other character previously utilized in making subgeneric and generic splits in this group, the alitruncal suturation, consists in its generalized condition of a weakly impressed, but fully ankylosed, semicircular line marking the promesonotal suture, and a straight, deeply cut transverse line at the site of the metanotum (metanotal groove; most *aculeaticoxae* \rightarrow *schmitti* morphocline members). In the *aculeaticoxae* \rightarrow *mordax* morphocline, effacement of one or both of these lines is erratic in its expression among species and species-groups, and intermediate stages exist in all possible combinations. There seems to be no practicable means of using this suturation for the definition of groupings worthy of formal generic or subgeneric names, and convergence here makes even the plotting of informal species-groups a more or less arbitrary matter.

In this group, there remains one aberrant species, *G. bispinosa* (Emery), that has previously been assigned to a separate subgenus, *Poncracantha*. *G. bispinosa* has very long propodeal spines, but *G. aculeaticoxae* has small, acute teeth in the same position, and in this and other ways, *aculeaticoxae* and the new species, *mecotyle*, are intermediate between *bispinosa* and the other *Gnamptogenys*. There remains the somewhat different form of the head in *bispinosa*; however, to anticipate the findings of

synonymy among the four generic groups for which evidence is offered below, the cephalic difference cannot well stand as a generic character when such a diverse group of other species is included in *Gnamptogenys*. In this, I only follow the evidence of the larvae, dealt with farther below.

HOLCOPONERA Group

Holcoponera has seemed like a compact and well-defined genus up to the time of this study, and I treated it as a genus in early drafts of this revision. The workers and females are similar to those of *Gnamptogenys* in their widespread and uniform costulate sculpture, but the workers have a more compact, dorsally convex alitrunk, crossed by a single suture (the promesonotal suture) which is deeply cut, and, at least to external appearances, completely separates the alitrunk into two parts. No such complete suturation is found in *Gnamptogenys sensu stricto*. The node of the petiole in worker and female is erect or inclined posteriad, usually more or less cupuliform to thick disciform. Added to the seemingly clearcut alitruncal difference in the worker there has previously been stressed a character in the forewing of the male, namely, the absence of the second and third abscissae of Rs; but this character is now known to occur in some species of undoubted *Gnamptogenys* as well. G. C. and J. Wheeler found the larvae of *Holcoponera* distinct from the related genera in that the head hairs were branched or bifurcate, whereas those of the related genera examined had simple head hairs. This character may eventually prove useful in segregating a generic group that could bear the name *Holcoponera*, but at the present time, its usefulness is greatly restricted by the fact that only a very few species of "higher ectatommines" have been examined in the larval stage. Of these few species, none are particularly "critical" in problems involving generic limits, and among them are none of the species that seem to be intermediate between *Holcoponera* and the other "higher" genera. Such species do exist, as I found to my great inconvenience at a time when I thought I had this revision just about completed, except for minor details.

In speaking of the connections I have discovered between *Holcoponera* and other groups, it should first be emphasized that

Holcaponera is not as large a genus in number of species, races and varieties as Santschi and others have considered it to be, nor is it quite as homogeneous a group as some, including myself, have thought. The first steps toward this realization were made in a recent paper (Brown, 1957) in which several forms were synonymized, two new species were described, and a species formerly placed in *Rhopalopone* (*relicta* Mann) was transferred into *Holcaponera*. Of the two new species added, one, *H. acuta*, was merely somewhat bizarre in possessing a petiole toothed at the summit; the other, *H. mina*, was seen to form a bridge between the more "typical" *Holcaponera* members (specifically, *H. strigata*) and *relicta*, hence the generic transfer. The species *relicta* was not transferred from *Rhopalopone* just because it fitted so very badly there, but because I felt that it was a little closer to *Holcaponera*, especially considering the fact that all other known *Rhopalopone* (synonym of *Stictoponera*, and therefore of *Gnamptogenys*, see below) species were Indo-Melanesian in distribution. It can be seen from this that the separation of *Holcaponera* from *Stictoponera* was more a matter of geography and convenience than morphological distinctness, but so long as no further difficulties arose, it seemed best to me to preserve the old and familiar generic arrangement for practical reasons. But further difficulties have arisen.

The species *reichenspergeri*, described by Santschi in *Acanthoponera*, was viewed belatedly, and proved not to belong to the genus in which Santschi had placed it. Instead, it was found to have characters allying it with *Holcaponera*, with the "*Rhopalopone*" group of *Stictoponera*, and with *Spaniopone*. The gastric sculpture [74] does not have the regular costulation of the other New World species, and all in all, I think we must realize that *reichenspergeri* is the last straw to be piled on the already considerable weight of evidence against the separation of the three major generic groups centered around *Gnamptogenys*, *Holcaponera* and *Stictoponera*. We can add to this evidence farther below in discussing the characters of new species in the *Stictoponera* Group, but before we leave the *Holcaponera* Group, it seems well to discuss briefly the monotypic genus *Spaniopone*.

Wheeler and Mann described *Spaniopone haytiana* as a proceratiine because of superficial resemblances to *Proceratium*, but Emery (1919, p. 107) soon pointed out the characters that allied *S. haytiana* with what I now call the "higher" ectatommines. Although Emery's comments were ignored by Wheeler in his 1922 classification, it is clear that Emery was correct in stating the relationships of *Spaniopone*. Among former *Holcoponera*, two species, *minia* and *relicta*, make approaches to *Spaniopone* in several respects, as does the omniparent *reichenspergeri*. If *haytiana* had been discovered in New Guinea or Java, rather than in Haiti, the chances are that it would have been placed in *Rhopalopone* from the beginning; certainly, there is nothing striking to separate it from the described "*Rhopalopone*" we already know from the Old World. Instead of a monotypic genus, it seems we have here just another moderately modified descendant of an old faunal element that was neither *Holcoponera* nor *Stictoponera*, but was ancestral to both stocks — in short, we have another intergradient species.

In view of the above facts and interpretations placed on them, it can be seen that we have in *Holcoponera* a stock that has been born and has radiated within the New World tropics, and that has attained a certain degree of adaptive success while evolving along a certain morphological pathway. There are some species, among them the common species, that we can point to and say, "There is *Holcoponera*." But we must not forget that there are other species of which we must say, "That could be *Holcoponera*, or it could be *Stictoponera*." Now, the question arises, should we recognize the new adaptive penetration that the *Holcoponera* stock has apparently made, and upon which its radiation is based, by granting the group generic status? Or should we emphasize instead the continuing existence of intergradient species, albeit frequently exceedingly rare and local ones, that still link the *Holcoponera* stock with other, independently radiating sister groups? I take the second choice because I believe that it is the most practical one. If we separate *Holcoponera* by drawing an arbitrary line around it, we shall never rest easy about distinguishing, or keying, or making biological statements about, the groups sundered in this way. The claim is often made that genera with many species become

“unwieldy” — although it is never stated just how one gains by splitting such a genus on arbitrary lines into two or more genera, or, worse, into subgenera. We have only to look at the generic classification of the birds, or, within the ants, at the subgeneric classification of *Camponotus*, to see where such arbitrary splitting leads.

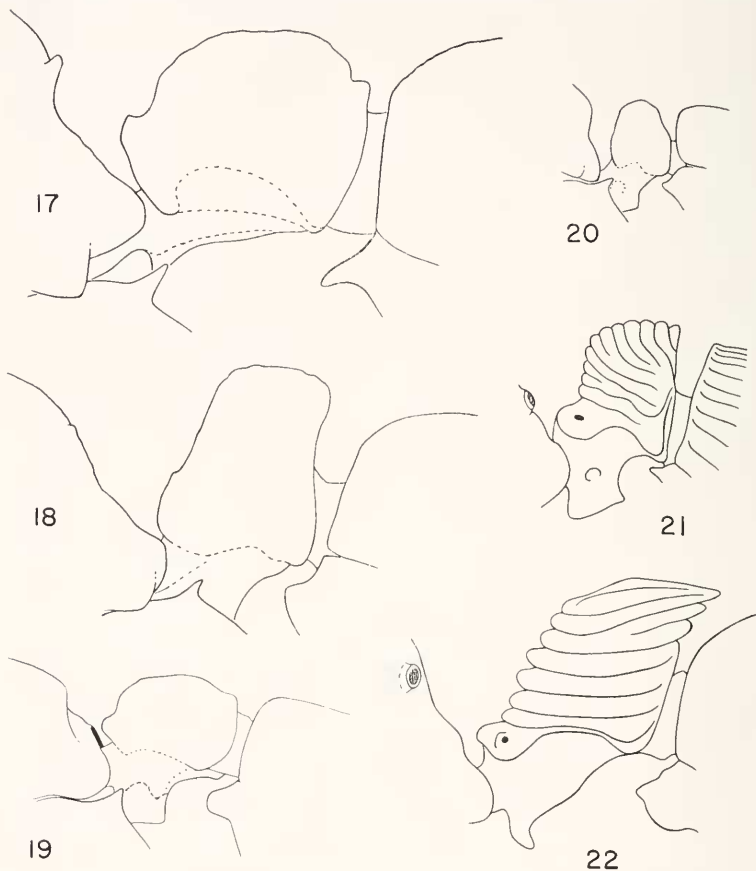
I feel that it is best to recognize now, while there are still few enough species known in the ectatommine tribe for one man to see and assimilate in one revisionary effort, that the old generic limits are mostly fading under the accession of new species, rather than the reverse. There is every reason to believe that many more species exist, unknown, and it is from the ranks of these rare and local forms that so many of our intergradient species come. We shall do the future discoverers of these forms a service if we give them a reasonably clear choice among a few large- and medium-sized genera instead of presenting them with a welter of small genera, none of which are sharply defined. And, just as important on the theoretical level, we shall be defining our genera in the way that is closest to objectivity, by stressing the gaps left when the intergrades die out. This is not, however, meant to discourage the search for new characters that may lead to new phylogenetic concepts and to new and more objective generic splits.

STICTOPONERA Group

The genus *Rhopalopone*, already discussed under the *Holcoponera* Group, above, is clearly a key group in ectatommine classification. Due to an extraordinary series of oversights, Emery, Forel, Wheeler and Mann all missed the extra tooth on the tarsal claws of (most) *Rhopalopone* species, and therefore continued to classify this genus in subtribe Typhlomyrmicini (see introductory section), apart from *Stictoponera* and *Wheeleripone* — the genera with which it is actually so closely allied as to be inseparable on any rigorous basis.

Another character supposedly distinguishing *Rhopalopone* was its possession of a fairly well defined funicular club; but this character is rendered worthless by the fact that club distinctness grades through without regard for the old generic limits between

Rhopalopone and *Stictoponera*. Mann's diagnosis of *Wheeleri*-*pone* and Wheeler's 1922 key to the ectatommine genera grant unwarranted value to the state of the alitruncal suturation and



Figures 17-22. *Gnamptogenys* spp., workers, side views of petioles and adjoining structures. Fig. 17, *G. biroi* (Emery) from near Sogeri, Papua (ex *Stictoponera*). Fig. 18, *G. panda* (Brown) from near Muping, Sikang Prov., western China (ex *Stictoponera*). Fig. 19, *G. chapmani* sp. nov., holotype. Fig. 20, *G. epinotalis* (Emery) from the Huon Peninsula, New Guinea, Wilson No. 931 (ex *Rhopalopone*). Fig. 21, *G. mina* (Brown), paratype (ex *Holcoponera*). Fig. 22, *G. acuta* (Brown), paratype (ex *Holcoponera*). Figs. 17-20 are all drawn to the same scale; Figs. 21 and 22 drawn to a very slightly larger scale.

to the degree of undercurvature of the gaster; actually, these traits are graded in degree, and differ by species rather than by genera. A review of almost all the Old World species shows clearly that the characters so far employed will not separate *Rhopalopone*, *Stictoponera* and *Wheeleripone* as generic entities. If we look at all the species of this group together, we can see better whether a division is necessary.

The first thing one notes is that there are two extremes of nodal form among the species. In *coralis* and relatives, the petiolar node is low and paniform (Figs. 17, 19), while in all the former *Rhopalopone* species examined, the node is erect and more or less anteroposteriorly compressed, even unto the form of a thick, blunt scale (Fig. 20). In addition, the *Rhopalopone* species are quite small, and the *Stictoponera* species described up to now have been considerably larger. However, we must note the following exceptions.

The species *taivanensis* and *panda* combine *Rhopalopone* nodes (Fig. 18) with *Stictoponera* size. The new species *chapmani* (Fig. 19) is typically *Stictoponera* in form of node, but is in the *Rhopalopone* size range. In *Wheeleripone*, *albiclava* would fall into *Stictoponera* in all characters, *crenaticeps* and *aterrima* fit best in *Rhopalopone*, and *lucida* is in between. I think this summary of the status of the diagnostic characters should serve as convincing proof of the futility of trying to separate the *Stictoponera* Group species as genera or subgenera. It is an equally difficult matter to separate these Old World forms from the New World ones. In the matter of sculpture, for instance, one finds that the new species of the *Stictoponera* Group from New Guinea (*G. grammodes*, and certain of the *Rhopalopone* species) approach, in the extent of their costulate or striate sculpture, the New World *Gnamptogenys*. Then, how does one separate *Spaniopone haytiana* from the smaller *Rhopalopone*? Or the latter from Mann's *relicta* of Brazil? Or Borgmeier's *Alfaria striolata* (Brazil) from the Old World *Stictoponera*? I think that the answer must be that we cannot separate these species or groups of species into genera or subgenera on the presently recognized characters.

ALFARIA Group

As I shall show in my species-level treatment of this group [65], Mann's genus *Opisthoscyphus* was founded on an artist's misrepresentation of the species formerly known as *Alfaria minuta* Emery. It is easier to eliminate this name than to account for the position of *Alfaria* as a genus. Of the nine species described in *Alfaria*, only four appear to stand at present. *A. simulans*, *A. bufonis* and *A. minuta* share as a characteristic the extremely inflated second gastric segment, but *A. striolata* has a less strongly developed second gastric segment, in this respect coming much closer to some species of the former genera *Stictoponera*, *Rhopalopone* and *Paracetatomma*. In its sculpture also, *A. striolata* is more typical of *Stictoponera*, and, in fact, *striolata* connects the other three valid *Alfaria* species so broadly to *Gnamptogenys* that I am forced to still another generic synonymy. This is the way generic revisions in the ants seem often to end; when I began this section, I would have bet on *Alfaria* as the most firmly founded and most distinct of the ectatommine genera, and I gave up the idea of generic distinctness for the group only when I first saw Father Borgmeier's *striolata*.

This completes the survey of the four groups of higher ectatommine genera. I think I have made a reasonable case for the synonymy of the genera and subgenera within each group, and it also now seems plain that no clear distinction exists among the groups, at least so far as we now know. Following the evidence as I see it, I have assigned all of these generic and subgeneric names to the synonymy of *Gnamptogenys*. This synonymy is set down with the greatest reluctance, and with the hope that some future study based on better material may establish a clear division of the species.

The species now falling in *Gnamptogenys* are very various, as might be expected by the former large number of genera and subgenera now included in the concept; however, there are as many features of homogeneity among these species as there are of heterogeneity. The *Gnamptogenys* species run for the most part to compact, heavily sclerotized forms. The size is small to medium-large, and the eyes of the workers range from minute to large. The shapes of the head and body are rather conservative, and never really bizarre, although the elongate mandibles

of the *schmitti* and *mordax* groups are unusual modifications of the triangular type found in most species. No distinct scrobes are formed to receive the antennae, and the clypeus is present and distinct as a broad, convex shield extending across the front of the head over the mandibles. Frontal carinae horizontal and with distinct, horizontal lobes roofing to some extent the antennal insertions. The eyes are usually placed near or behind the middle of the sides of the head, rarely absent. Antennae 12-segmented, with or without a club at the apex of the funiculus. Palpi of worker and female segmented 3,2 or 2,2. The 3,2 formula has been found in workers or females of *aculeaticoxae*, *alfaroi*, *annulata*, *bispinosa*, *chapmani*, *concinna*, *coxalis*, *menadensis* and *schmitti*, although the basal segment is short and very easily missed. A few species, notably *mordax* and close relatives, have lost one maxillary segment (perhaps the basal and second segments have fused), so that they now have a formula of 2,2. The former *Holcaponera* species, including *relicta*, *porcata* and forms of the *striatula* complex, all actually dissected, have formulae of 2,2, with the basal segment of the maxillary palp compressed and triangular, the free angle bearing a stout sensillum; the apical segment is long, slender and weakly curved. *G. minuta* (formerly *Alfaria m.*) has a formula of 1,2, *teste* Borgmeier, 1957:117.

The alitrunk is compact, and usually has a simple dorsal outline seen in profile, either convex or straight, rarely with a deeply impressed metanotal groove. Either the promesonotal suture or the metanotal groove, or more rarely both, may be developed to varying degrees, but the promesonotal suture, even when apparently completely separating the alitrunk into two parts (as in many former *Holcaponera*), seems to confer little or no flexibility upon the alitrunk. The propodeum may have a distinct declivity, or it may merge into the dorsal surface. The propodeum usually is unarmed, but small paired teeth are present in a few species, and these reach large size in *bispinosa*. A character of importance occurs on the dorsal face of the posterior coxae, each of these having a distinct tooth, spine or tubercle. This armament of the hind coxae is exclusive to the genus *Gnamptogenys*, and is lacking in only a few species scattered through different groups, so that it seems very likely that it is a primitive

trait secondarily lost in these species. The tarsal claws of each leg usually bear each a median or subbasal tooth, which may be difficult to detect except at very high magnifications in ideal silhouette against a brightly lighted background; in *epinotalis*, the extra tooth appears to be absent from the middle and hind tarsi, but is present on each fore tarsal claw. The extra tooth is well developed in the larger species, but tends to be inconspicuous in the smaller, cryptobiotic forms.

The petiolar node varies in form (Figs. 17-21, 42) from low paniform to thick disciform; a few species have the summit produced posterodorsally as a blunt tooth (Fig. 22). The form of the gaster varies with the species group; usually the postpetiole is separated from the succeeding (second gastric) segment by a very distinct constriction, and the latter segment is more or less distinctly undercurved. The remaining apical segments are reduced and more or less retractile within the second gastric segment. A functional sting is always present in the castes of the female sex.

Sculpture in *Gnamptogenys* species is based on a thick, heavy integument, so that figures can be and often are deeply cut and bizarre. The New World species are mostly covered with costulate or striate sculpture of a very regular and striking kind, whereas in the Indo-Melanesian species, striate and costulate sculpture is either absent or present over only limited areas of the body, and deep-set, umbilicate foveolae are often substituted. In the smaller, cryptobiotic species of both continents, the sculpture tends to become shallower and finer, and punctation may become mixed with striation or rugulation on the same surfaces.

Pilosity is normally simple and fine, the hairs being of uneven lengths, erect or suberect, and usually fairly abundant but not overly conspicuous. Smaller hairs may form a pubescence of the subappressed kind over parts of the appendages or other limited areas of the body.

Color of the worker and female castes varies from jet black, sometimes with contrasting light-colored appendages or sections of appendages, to testaceous in some small cryptobiotic species. The adults take a long while to develop full pigmentation, so that a full range of yellow and reddish examples may occur in the nest of a species that is definitively black. This color problem has been the cause of considerable synonymy at the species level.

It is perhaps risky to generalize concerning the sexual castes, since these are known for only a fraction of the species; females are known for more species than are males, since the nests are frequently small and the females therefore not difficult to find and take. Most females are either known in the winged state or from apparently normally dealate queens, but a few species, particularly among the smaller ones, have ergatoid queens without wings or fully developed flight sclerites in the thorax.

The males are quite distinct from the female castes, and are always winged. The size is usually slightly smaller than the workers of the same nest, and the head is much modified from the female-worker plan. The eyes are very large, occupying often a major portion of the sides of the head. Mandibles usually remaining fairly well developed, triangular and with serial dentition, but possibly not importantly functional. The palpi usually have more segments than in the worker, and perhaps this is invariably true. The basic formula in the male is maxillary 5, labial 3, but in some species or individuals there may be variable reduction. Thus, the fourth and fifth maxillary palp segments are fused in *concinna*, but are still distinguishable, and Kusnezov (1954:34) claims that the *triangularis* male has a formula of 4, 2. The notauli and parapsidal furrows are well developed (so far as known), and the scape is shorter, usually very much shorter, than the funiculus, appearing much the same as one of the longer funicular segments. The genitalia are retractile, or largely so, but the genital capsule is usually extruded in the available material. The parts are heavily sclerotized and rather simple, resembling the corresponding pieces of *Myrmica* so far as investigation has gone. The subgenital plate is unremarkable, being usually narrowly rounded and pubescent at its apex. However, very few species have been given more than a very superficial examination.

Wings similar in male and female, usually of the "complete" type, with all basic formicid elements in the forewing except the first radial crossvein. In some species (e.g., *G. mordax*, Brown and Nutting, 1950: pl. 8, fig. 5) Mf2 is completely contracted, and in quite a few others (*Holcaponera* Group), Rsf2+3 has disappeared as well.

The male sculpture is usually much reduced as compared to that of the corresponding workers, and is often largely effaced to give smooth, shining areas of wide extent, particularly over alitrunk and gaster. Otherwise, the sculpture is often a feeble and much less regular version of the corresponding worker's. The pilosity is little different from that of the female castes, but the color is often darker. Males are often taken separately at light, and in this case, it is usually impossible to determine to what worker-based species they belong, unless previous association has been made from nest material. Furthermore, we know very little about variation in the males, either individual or geographic, and it seems from the present evidence that this sex is not going to play a very important role in the taxonomy of the group. Final judgment on this matter, however, will have to rest on closer examination of a much more nearly representative sample of the species.

The larvae of species now included in *Gnamptogenys* are described by G. C. and J. Wheeler in their "Ant larvae of the subfamily Ponerinae" (1952a, pp. 121-124, 127-128, 132-134, pls. 3-5), and the generic affinities discussed in Part II of the same work (1952b, pp. 657-660).

As limited here, *Gnamptogenys* is known from two areas: one in the Old World, from Ceylon and western China to Fiji; and the other in the New World, from Texas to Tucumán and Buenos Aires, including Hispaniola in the Antilles. It seems safe to consider the genus a part of the "Old Endemic" fauna of South America, present there at the beginning of the Tertiary. Some of the imperfectly known fossils of the Tertiary (Oligocene) in Europe and North America are close to *Gnamptogenys*, and at least one does actually belong to the genus. Like *Heteroponera*, the Old and New World branches of *Gnamptogenys* show some separate radiation, but without loss of the linking species, particularly the small "*Rhopalopone*" forms.

We know very little about the biology of *Gnamptogenys* species, since many of them are rare and secretive in habits. Most of the species are restricted to moist tropical forests, where they nest mostly in rotten wood or in the soil; a few are semi-arboreal nesters in epiphyte "peat," at least facultatively so. Usually, the colonies consist of only a few individuals, probably

in most cases under 100, and frequently under 50. The queen is usually a dealate, more rarely an ergatogyne, and some colonies may have several reproductive females. The food probably consists mostly of small arthropods; Mann (1934:177-178, pl. 6) found *schmitti*, a long-mandibulate species, preying on millipeds in Haiti, and it seems likely that other specialized types of mandibles in the genus reflect prey preferences as yet unknown.

GNAMPTOGENYS species

Only new synonymy is listed here. Old synonyms can be found in Emery, 1911; Santschi, 1929c; Brown, 1954c, 1957. The new combinations are marked with an asterisk (*). Following the grand list, the trivial names are listed again in the genera or subgenera in which they stood prior to this publication; the order is that of the grand list, and all names are listed, whether synonyms or not.

- (P) *aculeaticorax* (Santschi), 1921:81. * Panama to Bolivia [45, 73]
- (P) *acuminata* Emery, 1896:50. Amazon-Orinoco drainage [43]
- (T) *acuta* (Brown), 1957:491. * Bolivia, Peru [46, Fig. 22]
- (T) *albiclava* (Mann), 1919:283. * Solomons: Ysabel I.
- (P) *alfaroi* Emery, 1894:145. Costa Rica [50]
- (P) *annulata* Mayr, 1887:543. se. Brazil, Bolivia n. to C. Amer. [44]
- (P) *arcuata* (Santschi), 1929c:457. * se. Brazil [79]
- = *regularis* (Santschi), 1929c:457, nee Mayr, 1870. * n. syn.
- (T) *aterrima* (Mann), 1921:411. * Fiji
- (T) *banksi* (Wheeler), 1930:10. * Panama
- (P) *bicolor* (Emery), 1889:493. * se. Asia [47]
- (P) *binghami* (Forel), 1900a:317. * Burma, Borneo, Philippines [47]
- (P) *bispinosa* (Emery), 1890a:40. * Panama, Costa Rica [49]
- (P) *biroi* (Emery), 1902b:154. * N. Guinea [47, fig. 17]
- (T) *bruchii* (Santschi), 1922:241. * n. Argentina
- (T) *bufonis* (Mann), 1926:101. * s. Mexico [65]
- (T) *chapmani* Brown, sp. nov. Philippines [58, Figs. 19, 44]
- (P) *concinna* (Fr. Smith), 1858:103. Bolivia to C. America [57]
- = *romani* Wheeler, 1923a:2. n. syn.
- (T) = *semicircularis* Borgmeier, 1929:195. n. syn.
- (P) = *conica* Borgmeier, 1929:196. n. syn.
- (T) *continua* Mayr, 1887:544. s. Mexico to s. Brazil [56]
- (P) = *panamensis* Santschi, 1931:265. n. syn.
- (P) *costata* (Emery), 1889:494. * Tenasserim to Sumatra, Philippines [47]

- (T) *coxalis* (Roger), 1860:308. * Ceylon [47]
crassicornis (Forel), 1912a:51. * Sumatra [47]
(T) *crenaticeps* (Mann), 1919:285. * Solomons: Ysabel I.
(T) *cribrata* (Emery), 1900:311. * N. Guinea [53]
(P) *curtula* (Emery), 1896:44, 47. * s. Mexico, C. America [70, 79]
(P) = *stolli* (Forel), 1899a:7. * n. syn.
(T) *dammermani* (Wheeler), 1924:2. * E. Indies, Philippines [53]
(T) *diehli* (Forel), 1901a:372. * Borneo [53]
(T) *epinotalis* (Emery), 1897a:550. * N. Guinea [53, Fig. 20]
(T) *exarata* Emery, 1901:50. Amazon-Orinoco drainage [54]
(T) *gracilis* (Santschi), 1929c:468. * British Guiana
(T) *grammodes* Brown, sp. nov. Papua [60, Fig. 41]
(T) *haenschi* Emery, 1902a:27. Bolivia, Peru, Ecuador [51]
(T) *hartmani* (Wheeler), 1915a:390. * Texas [52]
(T) *haytiana* (Wheeler and Mann), 1914:11. * Haiti [63]
(T) *horni* Santschi, 1929c:475. n. status Panama to Bolivia [62]
(T) *interrupta* Mayr, 1887:543. C. America, ?S. America [55]
(T) *kalabit* Brown, sp. nov. n. Borneo [59, Fig. 43]
(P) *laevior* (Forel), 1905:7. * Java [47]
lucida (Mann), 1919:285. * Solomons: Malaita I.
(T) *luzonensis* (Wheeler), 1929:30. * Philippines [53]
(T) *macretes* Brown, sp. nov. Papua [61]
(?) *magnifica* (Santschi), 1921:81. * sw. Brazil [71]
(T) *major* (Emery), 1902b:154. * N. Guinea [53]
(T) *malacensis* (Mann), 1919:281. * Solomons: Malaita I. [53]
(T) *mecotyle* Brown, sp. nov. Bolivia [66, Fig. 42]
(T) *mediatrix* Brown, sp. nov. Brazil [78, Fig. 15]
(P) *menadensis* (Mayr), 1887:539. * E. Indies, Philippines [47]
(T) *menozi* (Borgmeier), 1928a:32. * se. Brazil [64, 73]
(T) *mina* (Brown), 1957:494. * Bolivia, Peru [46, 73, Fig. 21]
(T) *minuta* (Emery), 1896:106. * S. and C. America [65]
(T) = *emeryi* (Forel), 1901b:326. * n. syn.
(T) = *scabrosus* (Mann), 1922:5. * n. syn.
(P) = *mus* (Santschi), 1931:265. * n. syn.
(T) = *panamensis* (Weber), 1940:80, nee Santschi, 1931. * n. syn.
(T) = *carinata* (Weber), 1940:82. * n. syn.
(P) *mocleri* (Forel), 1912b:34. * se. Brazil [81]
= *splendens* (Santschi), 1929c:450. * n. syn.
(T) *mordax* (Fr. Smith), 1858:98. C. and S. America [69]
(P) = *nodosa* (Latreille), 1802:217. n. syn.
(P) = *purcensis* Forel, 1912b:33. n. syn.
(T) = *sebastiani* Borgmeier, 1937:220. n. syn.
(T) *nigrifrons* Borgmeier, 1948:199. Peru
(T) *panda* (Brown), 1948a:263. * w. China [48, Fig. 18]

- (P) *pleurodon* (Emery), 1896:47. * Amazon drainage [71, 72]
 (P) = *emeryi* (Santschi), 1929c:463, nec Forel, 1901. * n. syn.
 (P) = *recta* (Santschi), 1929c:465. * n. syn.
 (P) = *vidua* (Santschi), 1929c:467. * n. syn.
 (P) *porcata* (Emery), 1896:48. * Costa Rica [71]
 (T) *posteropsis* (R. Gregg), 1951:77. * Sumatra, Philippines [47]
 (T) *rastrata* (Mayr), 1866:890. * se. Brazil [73, Fig. 16]
 (T) *regularis* Mayr, 1870b:965. s. Mexico to Paraguay [68]
 (P) = *splendida* Pergande, 1895:871. n. syn.
 (P) = *fiebrigi* Forel, 1909:253. n. syn.
 (T) *reichenspergeri* (Santschi), 1929b:274. * se. Brazil [74]
 (T) *relicta* (Mann), 1916:403. * Matto Grosso [46]
 (P) *rimulosa* (Roger), 1861a:18. se. Brazil [75]
 (?) *rustica* (Santschi), 1929c:446. * Paraguay [79]
 (P) *schmitti* (Forel), 1901a:334. * Haiti [83]
 (T) = *minor* (Wheeler), 1936:195, nec Forel, 1900. * n. syn.
 (T) *schubarti* (Borgmeier), 1948:198. * se. Brazil [64, 73]
 (T) *semiferox* Brown, sp. nov. Dominican Republic [77, Fig. 14]
 (P) *simplex* (Emery), 1896:48. * C. America [46]
 (?) *simplicoides* (Forel), 1908:341. * se. Brazil [79]
 (T) *simulans* (Emery), 1896:42. * C. America [65]
 (?) *spiralis* (Karawajew), 1925:79. * Java [47]
 (P) *striatula* Mayr, 1883:32. S. America, Jamaica, etc. [79, 46]
 (P) = *brasiliensis* (Emery), 1902c:181. * n. syn.
 (P) = *angustiloba* (Forel), 1908:341. * n. syn.
 (P) = *angustipleura* (Forel), 1908:342. * n. syn.
 (P) = *paulina* (Forel), 1908:342. * n. syn.
 (T) = *pernambucana* (Santschi), 1929c:452. * n. syn.
 = *calcarata* (Santschi), 1929c:452. * n. syn.
 = *hybrida* (Santschi), 1929c:455. * n. syn.
 (P) *strigata* (Norton), 1868:4. * s. Mexico to Honduras [70, 80]
 (T) *striolata* (Borgmeier), 1957:116. * se. Brazil [65]
 (P) *sulcata* (Fr. Smith), 1858:99. C. America to e. Brazil [82]
 (P) = *lineata* Mayr, 1870b:965. n. syn.
 (P) = *cearensis* Forel, 1912b:33. n. syn.
 (T) = *nitens* Mann, 1916:407. n. syn.
 (T) = *ypirangensis* Borgmeier, 1928b:60. n. syn.
 (T) = *bufonum* Weber, 1938:208, nec *bufonis* Mann, 1926. n. syn.
 (T) *taivanensis* (Wheeler), 1929:32. * Formosa [48]
 (T) *teffensis* (Santschi), 1929c:449. * Amazon-Orinoco drainage [81]
 (T) = *concinna* Santschi, 1929c:450, nec Fr. Smith, 1858. * n. syn.
 (P) *tornata* (Roger), 1861:15. s. Mexico to Colombia [67]
 (P) = *ericae* Forel, 1912b:33. n. syn.

- (P) *tortuolosa* (Fr. Smith), 1858:99. Amazon-Orinoco to Ecuador [76]
 (P) = *quitensis* Forel, 1920:133. n. syn.
 (P) *triangularis* Mayr, 1887:544. n. Argentina to se. Brazil [73]
 = *richteri* (Forel), 1913c:203. * n. syn.
 (?) *trigona* Emery, 1905:114. * se. Brazil [73]
 wasmanni (Santschi), 1929c:466. * Pará, Panamá [79]
 (T) = *isthmica* (Santschi), 1929c:467. * n. syn.
 (T) *wheeleri* (Santschi), 1929c:488. * Costa Rica [79]
 (P) = *mayri* (Santschi), 1929c:453. * n. syn.

*New Combinations in Gnampptogenys

- From *Stictoponera*: *bicolor*, *binghami*, *biroi*, *costata*, *coxalis*, *crassicornis*, *laccior*, *menadensis*, *panda*, *posteropsis*, *spiralis*, *taivanensis*.
 From *Rhopalopone*: *cribrata*, *dammermani*, *diehli*, *epinotalis*, *luzonensis*, *major*, *malaensis*. Note: *R. relictata* Mann was transferred to *Holcoponera* by Brown, 1957:491. *R. simillima* (Fr. Smith) *sensu* Emery has been transferred to *Prionopelta* (Amblyoponini) by Brown, 1953b:12.
 From *Wheelcripone*: *albiclava*, *aterrima*, *crenaticeps*, *lucida*.
 From *Ectatomma* (*Poncracantha*): *aculeaticoxae*, *bispinosa*.
 From *Acanthoponera* (*Anacanthoponera*): *reichenspergeri*.
 From *Spaniopone*: *haytiana*.
 From *Emeryella* s. str.: *schmitti*, *minor* Wheeler, *nec* Forel.
 From *Emeryella* (*Barbourella*): *banksi*.
 From *Holcoponera*: *acuta*, *arcuata*, *regularis* Santschi, *nec* Mayr, *curtula*, *stolli*, *gracilis*, *magnifica*, *mina*, *moelleri*, *splendens*, *pleurodon*, *emeryi* Santschi, *nec* Forel, *recta*, *vidua*, *porcata*, *relictata*, *rustica*, *simplex*, *simplioides*, *brasiliensis*, *angustiloba*, *angustipleura*, *paulina*, *pernambucana*, *calcarata*, *hybrida*, *stigmata*, *teffensis*, *concinna* Santschi, *nec* Fr. Smith, *wasmanni*, *isthmica*, *wheeleri*, *mayri*. *H. striatula* Mayr was originally described in *Gnampptogenys*.
 From *Alfaria*: *bufonis*, *minuta*, *emeryi*, *mus*, *panamensis* Weber, *nec* Santschi, *carinata*, *sinulans*, *striolata*.
 From *Opisthosecyphus*: *scabrosus*.
 From *Ectatomma* (*Parectatomma*): *hartmani*, *mcnozzii*, *rastrata*, *schubarti*, *richteri*, *trigona*. The species *triangularis* was originally described as a *Gnampptogenys*.
 From *Commateta*: *bruchii*.
 From *Tammotea*: *concinna* (Fr. Smith), placed here only by Santschi.

Key to New World species of Gnampptogenys — workers

1. Propodeum armed with a pair of long, slender spines, normally at least as long as the distance between the inner sides of their bases (C. America) *bispinosa* (Emery)
- Propodeum unarmed, or with a much smaller pair of teeth 2.

2. Second postpetiolar (second gastric) segment very strongly vaulted in the manner of *Proceratium*, and much inflated, its maximum cross-section diameter much greater than that of postpetiole 3.
3. Second postpetiolar segment usually (but not always) less strongly vaulted; its maximum cross-section diameter subequal to, or smaller than, that of postpetiole 5.
3. Size smaller, head width < 1.0 mm., length of alitrunk (WL) < 1.6 mm.; superficial sculpture consisting of extremely fine, opaque, amorphous or subgranulose roughening (C. and tropical S. America)
minuta (Emery)
 Size larger, head width > 1.0 mm., WL > 1.6 mm.; superficial sculpture consisting of extremely fine, even striolation, giving a silky luster to the integument 4.
4. Alitrunk with a well-defined and distinctly impressed metanotal groove (s. Mexico) *bufonis* (Mann)
 Metanotal groove obliterated on dorsum of alitrunk (C. America)
simulans (Emery)
5. Postpetiole completely transversely striolate both above and below; very small, yellowish *Proceratium*-like species with minute eyes (Haiti) ...
haytiana (Wheeler and Mann)
 Postpetiole predominantly longitudinally costulate or striate over the dorsum, or at least with some longitudinal striation or costulation in the central or posteromedian part of the disc 6.
6. Pronotum separated from remainder of alitrunk by a very distinct suture, completely breaking the sculpture 7.
7. Promesonotal suture absent across the dorsum, or indicated by an impressed line that does not break the sculpture 18
7. Alitrunk with sculpture on dorsum partly replaced by extensive smooth, shining areas 8.
8. Dorsum of alitrunk sculptured (usually costulate or striate) throughout 9.
8. Postpetiolar dorsum (and that of succeeding segment) coarsely and regularly costulate in a longitudinal direction; color (of types) red-brown (w. Brazil) *relicta* (Mann)
 Postpetiolar dorsum (and that of succeeding segment) with irregular striation arching over a shining, obscurely longitudinally striate postero-medial area; color deep piceous to black (se. Brazil)
reichenspergeri (Santschi)

9. Compound eye small, its maximum diameter $<$ the greatest thickness of the apical funicular segment; postpetiole truncate at base, the smooth anterior face separated from the costulate dorsal surface by a rim or margin (Fig. 21) (Bolivia, Peru) *mina* (Brown)
Compound eye larger, its maximum diameter equalling or exceeding the greatest thickness of the apical funicular segment; postpetiole with anterior face costulate and curving directly into dorsal surface (Fig. 22) 10.
10. Petiolar node terminating in a distinct flattened posterapical tooth or process, grossly acute, especially in lateral view; ventral process of petiole triangular, tapering to a narrow, slightly recurved lobe or tooth (Fig. 22) (Bolivia, Peru) *acuta* (Brown)
Petiolar node not terminating in a distinct posterapical tooth or process, though the posterior apex may project slightly backwards; ventral process of petiole differently shaped (not as in Fig. 22) 11.
11. Ventral surface of postpetiole predominantly transversely costulate (C. America) *simplex* (Emery)
Ventral surface of postpetiole predominantly longitudinally or obliquely costulate 12.
12. Funicular segment I (basal segment) as long as or slightly longer than II and III taken together; small species (s. Mexico, C. America) .. *strigata* (Norton)
Funicular segments II and III relatively longer (II particularly); II and III together longer than I 13.
13. Larger species, with long antennae, scape length (excluding basal neck) normally > 1.08 mm. 14.
Smaller species, with shorter antennae, scape length normally < 1.08 mm. 17.
14. Petiolar node more or less tilted posteriad in side view, the posterodorsal angle sharply rounded and slightly overhanging the posterior face; ventral process triangular or rounded, unlobed 15.
Petiolar node erect, in side view the posterodorsal angle not very much more sharply rounded than anterodorsal angle, and not overhanging posterior face; ventral process bilobed, or at least tending to form a posterior heel or corner 16.
15. Sculpture fine, more than 30 costulae between eyes; anterior $\frac{1}{3}$ to $\frac{1}{2}$ of postpetiolar dorsum transversely-arched costulate; head narrow, especially across occiput, occipital angle as seen from side sharply rounded, subauriculate (Guianas) *gracilis* (Santschi)
Sculpture coarser, less than 30 costulae between eyes; at most a very

narrow band of transverse costulae along the anterior margin of postpetiole; head broader, occipital angle as seen from side gently rounded, not auriculate

(Costa Rica) *porcata* (Emery)

(sw. Brazil) *magnifica* (Santschi)

16. Antennae (and individual segments) more slender, the penultimate segment distinctly longer than broad (se. Brazil) *moelleri* (Forel)
Antennae (and individual segments) thicker, the penultimate segment as thick as or thicker than long (Amazon-Orinoco drainage)

teffensis (Santschi)

17. Petiolar node and ventral process usually more or less as described in first lug of couplet 14, ventral process usually a tapered triangle (Panama to Bolivia) *pleurodon* (Emery)

vasmanni (Santschi)

Petiolar node usually as described in second lug of couplet 14: ventral process bilobed, square-cut, or with a single rounded lobe

group of *striatula* (Emery)

(The *striatula* group includes six nominal species: *arcuata*, *curtula*, *rustica*, *simplicoides*, *striatula* and *whecleri*, of which perhaps two to four are good species. One extreme of variation is "typical" *striatula*, with fine costulation and a square-cut or emarginate ventral petiolar process [S. America, Antilles]; another fairly well-marked form is *curtula*, with posterior lobe of ventral process reduced to a broad convexity [s. Mexico, C. America]. These and other forms are linked by intergrades; apparently character displacement is involved.)

18. Mandibles elongate and falcate or subfalcate, their inner margins in large part very distinctly concave, only their apical portions meeting or crossing when mandibles are closed (Figs. 14, 15) 19.

Mandibles triangular, with distinct apical and basal angles separated by a rounded basal angle, and the apical margin straight or very feebly concave (Fig. 16), or else the apical and basal margins continuous with each other in one broad convexity bearing low, vaguely double-ranked tubercles 22.

19. Mandibles exceedingly long and slender, each with an exposed straight-line length $>$ length of head proper (HL) (Haiti) ... *schmitti* (Forel)
Mandibles shorter and relatively broader, straightline length of each mandible $<$ HL 20.

20. Inner borders of mandibles each with only a short triangular tooth to represent the basal angle (Panama) *banksi* (Wheeler)
Inner borders of mandibles each retaining the basal angle as a low, broadly rounded lobe or flange lying basad of midlength (Figs. 14, 15) 21.

21. Mandibles longer (Fig. 14); propodeum unarmed, its declivity transversely costulate; sternum of postpetiole predominantly smooth and shining (Dominican Republic) *semiferax* sp. nov.
Mandibles shorter (Fig. 15); propodeum with a pair of short teeth, its declivity longitudinally costulate; sternum of postpetiole transversely to obliquely costulate throughout (se. Brazil, Pará) .. *mediatrix* sp. nov.
22. When head is seen in perfect full-face (dorsal) view, and the antennal scapes are laid back as straight as possible from their insertions, they either fail to reach, or just barely reach, but do not distinctly surpass, the part of the occipital border nearest to which they fall 23.
In same view, the antennal scapes when laid straight back from their insertions do distinctly surpass the posterior occipital border nearest to where they fall 33.
23. Dorsal surfaces of mandibles distinctly and continuously striate over the basal third or more of their length 24.
Dorsal surfaces of mandibles smooth and shining to the base, though sometimes with scattered punctures 25.
24. Larger species, head width across eyes > 1.2 mm.; mandibular striation extending from insertions to apices (Bolivia, Ecuador) *haenschi* Emery
Smaller species, head width across eyes < 1.0 mm.; apical half of mandibles smooth and shining (Texas) *hartmani* (Wheeler)
25. Dorsal face of propodeum predominantly or wholly transversely striate, although the anteriormost portion may sometimes bear sharply diverging oblique striation 26.
Dorsal face of propodeum predominantly longitudinally costulate or striate, continuing the longitudinal promesonotal sculpture straight back to at least the propodeal midlength, and usually beyond 27.
26. Large, long-headed species, head length (HL) > 1.7 mm.; when head is seen in perfect full-face view, occipital border evenly convex; blunt but distinct vestiges of paired teeth on the propodeal declivity (Costa Rica) *alfaroi* Emery
Smaller, more short-headed species, HL < 1.5 mm.; when head is seen in perfect full-face view, occipital border straight or feebly concave in the middle; propodeum absolutely unarmed (C. America to s. Brazil and Bolivia) *annulata* Mayr
27. Anterior margin of narrow anterior apron of clypeus (not to be confused with underlying labral outline) distinctly concave in the middle, and the lateral corners rounded 28.
Anterior margin of anterior apron of clypeus straight, or if shallowly concave, then terminating laterally in sharply rectangular corners ... 31.

28. Compound eye of worker large, its greatest diameter $>$ the maximum width of antennal scape 29.
Compound eye of worker small, usually consisting of only about 6-15 pigmented facets; greatest diameter less than, or at least not exceeding, maximum width of antennal scape 30.
29. Larger species, size and sculpture very variable, width of head across and including compound eyes $>$ 1.0 mm. (C. America, tropical S. America) *mordax* (Fr. Smith)
Smaller species, width of head across and including eyes $<$ 1.0 mm. (Peru, Guianas) *exarata* Emery
30. Medium-sized species, width of head across and including compound eyes $>$ 0.7 mm. (C. America) *interrupta* Mayr
Very small species, width of head across eyes $<$ 0.7 mm. (s. Mexico to se. Brazil, Jamaica) *continua* Mayr
31. Metanotal groove distinct and impressed, visible in all lights; sculpture fine, 38 or more costulae between compound eyes, 19 or more between frontal carinae (se. Brazil) *rimulosa* (Roger)
Metanotal groove absent or very indistinct, at best visible only in certain lights and views; sculpture coarser, $<$ 38 costulae between eyes, $<$ 19 between frontal carinae 32.
32. Larger species (usually HW $>$ 0.73, WL $>$ 1.25 mm.); petiolar node longitudinally costulate, at most only the lower part of the anterior face transversely costulate (s. Mexico to Paraguay) *regularis* Mayr
Smaller species (usually HW $<$ 0.73, WL $<$ 1.25 mm.); petiolar node with costulae arching transversely across entire anterior face, from top to bottom (Panama, Trinidad, Amazon-Orinoco drainage to Bolivia) *horni* Santschi
33. Large species, head width without eyes $>$ 2.0 mm.; color usually ferruginous; sculpture fine; petiolar node produced to a blunt posterapical point or tooth (C. into tropical S. America) *concinna* (Fr. Smith)
Small and medium species, head width without eyes $<$ 2.0 mm. 34.
34. Postpetiolar tergum with parallel chains of coarse punctures separated by irregular rugulae arranged in a pattern arching over a postero-median area of finer longitudinal costulation; succeeding segment strongly recurved and longitudinally costulate; eyes reduced (se. Brazil) *striolata* (Borgmeier)
Tergum of postpetiole (and of succeeding segment) evenly costulate, nearly always in a longitudinal direction; second postpetiolar segment more weakly downcurved 35.

35. Mandibles predominantly smooth and shining, with scattered punctures; striae or costulae, if present, restricted to basal third or less of length; transverse dorsal sutures of alitrunk obliterated, except in *G. nigrifrons* 36.
- Mandibles predominantly longitudinally costulate or striate; metanotal groove represented by a distinct narrow impressed line 41.
36. Size larger, head width without eyes > 1.3 mm. (Amazon-Orinoco drainage to Ecuador) *tortuolosa* (Fr. Smith)
- Size smaller, head width without eyes < 1.3 mm. 37.
37. Anterior clypeal apron with sharply angular free corners; mandibles sublinear, sharply downcurved, their basal and apical margins meeting through a single continuous convexity; petiolar node longer than broad to (rarely) very slightly broader than long 38.
- Anterior clypeal apron with rounded free corners; mandibles more or less triangular, the basal and apical margins distinct and separated by a distinct but rounded basal angle; petiolar node always distinctly broader than long 40.
38. Node of petiole seen from the side ending in a blunt point distinctly overhanging the posterior face (Amazon-Orinoco drainage)
- *acuminata* Emery
- Node of petiole seen from the side without a distinctly projecting posterodorsal point 39.
39. Head in back of antennal insertions black or nearly so; mandibles straw yellow, contrasting sharply with black of cranium; alitrunk, node and gaster varying from black to yellowish-ferruginous; costulae of propodeal declivity longitudinal (C. and tropical S. America)
- *sulcata* (Fr. Smith)
- Head yellowish to brown in color; mandibles dull yellow to brownish, usually lighter than cranial color, but not markedly contrasting with it; head and rest of body nearly concolorous; many workers from Central America and Mexico with costulae transverse across propodeal declivity (s. Mexico to Colombia) *tornata* (Roger)
- (*G. acuminata*, *G. sulcata* and *G. tornata* are often difficult to distinguish, and further material could well show them to be just variants of a single plastic species.)
40. Transverse sutural lines effaced on alitrunk dorsum, so that the surface forms one unbroken, very gentle convexity from pronotum to propodeal declivity; propodeal angles evenly rounded as seen from the side (n. Argentina) *bruchii* (Santschi)
- Metanotal groove impressed and distinct, separating propodeal dorsum into a convexity distinct from promesonotum; propodeal angles salient and more nearly rectangular as seen from side (Peru)
- *nigrifrons* Borgmeier

41. Petiolar node markedly longer than broad (Fig. 42); anterior pronotum covered by a broad band of transversely arching costulae (Bolivia) *mecotyle* sp. nov.
Petiolar node broader than long, as broad as long, or very slightly longer than broad; costulae longitudinal over the full pronotal length, only occasionally with one or two obscure transverse costulae at the junction of pronotum and cervix 42.
42. Size smaller, head width without compound eyes < 1.0 mm. (se. Brazil)
rastrata (Mayr)
?trigona Emery
Size larger, head width without compound eyes > 1.0 mm. 43.
43. Sculpture finer, usually > 26 costulae between compound eyes; size smaller, head width without eyes 1.25 mm. or less 44.
Sculpture coarse, usually 26 or less costulae between compound eyes; size larger, head width without eyes > 1.25 mm. 45.
44. Sculpture finer, petiolar node with 13-16 transverse costulae visible from above; node usually wider than long (s. Brazil to n. Argentina)
triangularis Mayr
Sculpture coarser, petiolar node with 11-13 transverse costulae visible from above; node usually not distinctly broader than long (Panama to Bolivia) *aculeaticoxae* (Santschi)
(*G. triangularis* and *G. aculeaticoxae* have mutually exclusive ranges so far as known; they are both variable in the diagnostic characters, and may possibly be mere geographical variants of a single species.)
45. Ventral process of petiole with a blunt or rounded anterior free angle and a salient, dentiform or subdentiform posterior free angle (Rio Grande do Sul, Paraná) *menozzii* (Borgmeier)
Ventral process of petiole with only the rounded anterior free angle or lobe developed; posterior angle absent or reduced to a simple low, broad convexity (S. Paulo, Rio de Janeiro) *schubarti* (Borgmeier)
(*G. menozzii* and *G. schubarti* may be part of the geographical variation of a single species.)

Key to Old World species of Gnampptogenys — workers

1. Second postpetiolar (second gastric) segment with tergum predominantly (usually longitudinally) costate or striate, this sculpture extending over the basal third or more of the exposed portion of the segment.
2. Second postpetiolar segment smooth, punctate, or otherwise sculptured; remnants of costation or striation, if present, peripherally distributed, and if found at base of segment, not extending beyond basal quarter.
- 7.

2. Compound eyes placed within the posterior quarter of the sides of the head, nearly at the posterior angles (Sumatra, Mindanao)
posteropsis (R. Gregg)
Centers of compound eyes placed anterior to posterior quarter of sides of head3.
3. Eyes small, each composed of 20 or less facets; petiolar node antero-posteriorly compressed, in the form of a thick scale, rounded above; body size smaller, head width (without eyes) < 0.80 mm. (N. Guinea) ..
major (Emery)
Eyes larger, each composed of many more than 20 facets; petiolar node low, rounded, paniform; body size larger, head width (without eyes) > 0.80 mm.4.
4. Eyes very large, occupying fully $\frac{1}{3}$ length of sides of head, their greatest diameter approximately = combined length of penultimate and antepenultimate antennal segments (N. Guinea)*biroi* (Emery)
Eyes not so large, occupying distinctly < $\frac{1}{3}$ length of sides of head, their greatest diameter distinctly < combined length of penultimate and antepenultimate antennal segments5.
5. Occipital angles as seen from the side each produced as a small, simple, narrowly rounded, lamellate lobe or margin, much narrower than compound eye; petiolar node distinctly transversely costulate its length; second postpetiolar tergum longitudinally finely costulate (or striate) over basal half to third, remainder smooth and shining (N. Guinea) ...
macretes sp. nov.
Occipital angle as seen from the side produced as a large, more or less fan-like lobe or "ear" with a narrow translucent margin, usually angled at both ends, lobe as wide as or wider than compound eye; petiolar node not transversely costulate, or with a few costules near posterior end; second postpetiolar tergum coarsely longitudinally costate (or fluted) for nearly its entire length6.
6. Sculpture finer, denser and more opaque, with noticeable development of longitudinal striation or costulation between punctures over head and alitrunk; costulae of postpetiole fine, close and distinct; funiculi slender, its segments III through VI longer than thick (Ceylon)
cozalis (Roger)
Sculpture coarser, striation absent or suppressed in favor of the coarse foveolae over head and alitrunk; costulae of postpetiole coarse and often indistinct, sometimes consisting merely of elongate welts between foveolae; funicular segments III through VI as thick as or thicker than long (Sumatra, Tenasserim to Mindanao)*costata* (Emery)

7. Postpetiole coarsely and very distinctly striate over tergum, intercostular punctures reduced in center of disc, larger on sides (N. Guinea)
grammodes sp. nov.
Postpetiole smooth, or punctate, or indefinitely rugulose; striation, if present, fine, indistinct and interrupted, subordinate to coarser punctures or other sculpture8.
8. Length of antennal scape (excluding basal neck) 0.87 mm. or more ...9.
Length of antennal scape (excluding basal neck) < 0.87 mm.14.
9. Petiolar node anteroposteriorly compressed, excluding ventral process, higher than long, with steep, high anterior and posterior faces (Fig. 18)10.
Petiolar node low, paniform, gently rounded above, longer than high, excluding ventral process (Fig. 19)11.
10. Gastric dorsum with fine, irregular interpunctural sculpture developed (rendering the surface more opaque) and reaching even to the center of the second postpetiolar tergum; color red-brown; posterior occipital corner as seen from the side terminating in a distinct (but variable) point or lobe (w. China) *panda* (Brown)
Gastric dorsum with interpunctural spaces smoother, more shining, especially the disc of the second tergum; color blackish-brown; posterior occipital corner as seen from the side evenly rounded, without lobe or point (Formosa) *taivanensis* (Wheeler)
11. Alitrunk almost completely smooth and shining, with scattered inconspicuous punctures; mesonotum coarsely and evenly longitudinally costate; four apical antennomeres ivory white, contrasting with rest of funiculus, which is ferruginous in color (Solomons) .. *albiclava* (Mann)
Alitrunk coarsely foveolate, including mesonotum; antennal club not white12.
12. Greatest diameter of eye subequal to greatest thickness of apical antennomere; body usually more or less concolorous brownish-red (Burma, Sumatra to Philippines) *binghami* (Forel)
(*G. crassicornis* Forel and *G. spiralis* Karawajew probably would run to *binghami*, but in these, the eye is placed in front of the middle of the side of the head. They may both be only variants of *binghami*, in which eye position varies.)
Greatest diameter of eye markedly > greatest thickness of apical antennomere; full adult color usually blackish or bicolored13.
13. Full adult color piceous to black over body; a narrow median strip on mesonotum smooth and shining (Sumatra to Celebes and Philippines) .
menadensis (Mayr)

Full adult color with gaster (and often the head) piceous, alitrunk much lighter, orange-ferruginous; median strip of mesonotum finely, indefinitely, longitudinally rugulose, more or less opaque (se. Asia to Java) .

bicolor (Emery)

14. Alitrunk smooth and shining dorsally (when clean), with separated punctures or foveolae15.
Alitrunk dorsally in large part (at least the pronotum) densely sculptured and more or less opaque, with or without definite punctures or foveolae 19.
15. Head with straight, parallel sides and rectangular occipital corners; eyes large and only gently convex, occupying about $\frac{1}{4}$ length of sides of head (Figs. 43, 44); antennal scapes short and thick, surpassing occipital margin by much less than their apical thickness 16.
Head with sides more or less convex, occipital corners rounded; eyes smaller, occupying $\frac{1}{5}$ or less of length of sides of head; antennal scapes longer and more slender, surpassing occipital margin by their apical width or more 17.
16. Size larger, head width (without eyes) > 0.70 mm. (Java)
laevior (Forel)
Size smaller, head width (without eyes) < 0.70 mm. (Philippines)
chapmani sp. nov.
17. Antennal funiculus bicolored, the four apical segments whitish in color, contrasting with the ferruginous color of the rest of the antenna (Solomons: Malaita I.) *lucida* (Mann)
Antennae concolorous ferruginous18.
18. Dorsum of head with coarse contiguous punctures, the median strip longitudinally costulate and subopaque (Fijis) *aterrima* (Mann)
Dorsum of head with punctures mostly separated by smooth, shining intervals; median strip almost free of punctures, smooth and shining (Solomons: Ysabel I.) *crenaticeps* (Mann)
19. Eyes large, occupying about $\frac{1}{4}$ length of sides of head; their greatest diameter $>$ greatest thickness of antennal scape (Fig. 43) (n. Borneo)
kalabit sp. nov.
Eyes small, occupying much $< \frac{1}{4}$ length of sides of head; their greatest diameter $<$ greatest thickness of antennal scape 20.
20. Second tergum of gaster (second postpetiolar segment) densely punctate, subopaque, the coarse punctures subcontiguous and separated only by vague longitudinal costulae (Solomons: Malaita I.) *malaensis* (Mann)
Second tergum of gaster with separated small punctures, the broad intervals smooth and shining21.

21. A broad median area extending over the anterior half or more of the propodeum smooth and shining (N. Guinea) 22.
 Propodeum completely sculptured, or at most with a very narrow, indefinite smoothed area limited to the anterior third of the dorsum (E. Indies, Philippines) 23.
22. Punctures of postpetiole large and deep, relatively few in number, separated by broad shining spaces; full adult color of body deep brownish-red *cribrata* (Emery)
 Punctures of postpetiole small, superficial and densely arranged, separated by narrow shining spaces, the total surface subopaque; full adult body color ferruginous yellow *epinotalis* (Emery)
23. Size larger, maximum pronotal width 0.38 mm. or more; full adult body color deep brownish-red, postpetiolar punctures large and deep
dammermani (Wheeler)
 Size smaller, maximum pronotal width < 0.38 mm., full adult color yellowish-ferruginous; postpetiolar punctures smaller and shallow
luzonensis (Wheeler)
 (According to the original description, *diehli* (Forel) would run to complet 23; Wilson has seen the type and finds it to differ from *dammermani*. Differences from *luzonensis* unclear.)

PROCERATIUM Roger

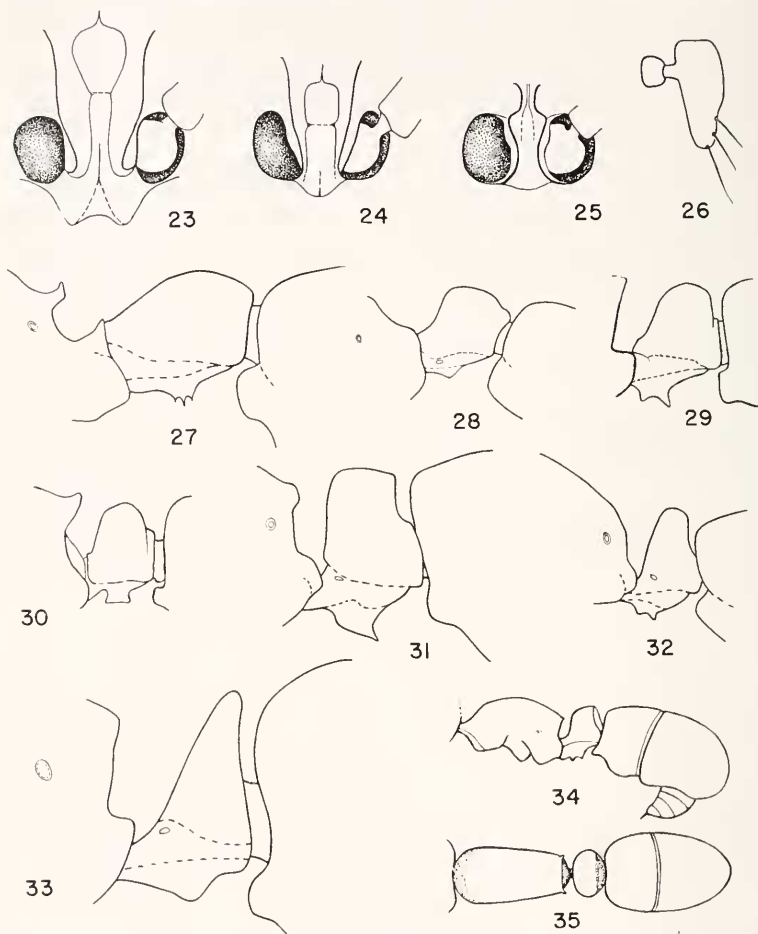
- > *Proceratium* Roger, 1863:171. Type: *Proceratium silaceum* Roger, 1863, monobasic.
- > *Sysphingta* Roger, 1863:175. Type: *Sysphingta micrommata* Roger, 1863, monobasic. Synonymy after Dalla Torre, 1893:18.
- > *Sysphincta* (!) Mayr, 1865:12, and most subsequent authors; emendation of *Sysphingta* Roger.
- > *Proceratium* subgenus *Sysphincta*, Forel, 1913a:212.

The genera *Proceratium* and *Sysphincta* have been relatively well known to specialists of the northern countries. Taking separately the Nearctic, European and Japanese representations of these two genera, it has previously been considered possible to separate them on the Emery-Wheeler key characters, thus:

Clypeus with an anterior median projection; petiole more or less nodiform *Sysphincta*.

Clypeus without an anterior median projection; petiole in the form of a thick erect scale *Proceratium*.

However, it seems that the protests of Forel (1913a) against this generic distinction have been overlooked. Forel stated that



Figures 23-35. *Proceratium* spp., workers, dorsal views of anteromedian part of head, all drawn to same scale. Fig. 23, *P. pergandei* (Missouri). Fig. 24, *P. melinum* (Italy). Fig. 25, *P. toschii* (holotype, Kenya). Figure 26, *P. croceum* (Alabama), detail of maxillary palpus, female. Figures 27-32. *Proceratium* spp., workers, side views of petioles and adjoining structures, all drawn to same scale. Fig. 27, *P. stictum*, sp. nov. (holotype, n. Queensland). Fig. 28, *P. micrommatum* (Veracruz). Fig. 29, *P. melinum* (n. Italy). Fig. 30, *P. toschii* (holotype). Fig. 31, *P. croceum* (Alabama). Fig. 32, *P. papuanum* (Malanda, n. Queensland). Fig. 33, *P. relictum*, female syntype (Fiji). Figures 34, 35. *P. arnoldi*, body, from sketches by Dr. G. Arnold, worker syntype (S. Rhodesia). Fig. 34, side view. Fig. 35,

for both the clypeal projection and nodal form characters there existed "all possible intergrades." Since that time, the number of species described has doubled, and some of the forms added are further intermediates in the two crucial characters. Other forms show extreme development of characters of either genus; *stictum* (Fig. 27, 45, 46) is a "super-*Sysphincta*," while *relictum* is a "super-*Proceratium*" (Fig. 33). It has been possible to assemble a representative series of species showing the gradualness of change from "super-*Sysphincta*" to "super-*Proceratium*" in nodal form (Figs. 27-35), and also illustrating nicely the loss of the median projection of the clypeus. Figure 46 shows the broad median clypeal lobe, apparently the generalized condition, still preserved in *stictum*. Figures 23 to 25 show the degeneration of the lobe into a bicarinate median projection in *pergandei* and allies (Fig. 23), then through the stage of fusion of the carinae to a unipartite projection in the *melinum* group (Fig. 24), and finally to the low vestigial flange of the African species *toschii* (Fig. 24) and *arnoldi* (Fig. 1), after which, in the remainder of the species, there is left no trace of the projection.

Other characters have been studied in the search for separatory features to distinguish two or more genera among the full array of species, but so far all characters appear to show gradation from one extreme to the other.

In mandibular dentition, one begins with a distinctly four-dentate masticatory border in *stictum* and follows the gradation through a number of species to the condition where two strong apical teeth remain, followed basad by an indefinite number of low, irregular denticles or else a relatively smooth margin. In some of the *Sysphincta* species, the undercurving of the principal (second) gastric segment is extreme, but this character again grades over by easy steps to a less extreme condition. The same applies to the palpal segmentation, as far as known [84]. Too few larvae are yet known for these to be of any help with the classification, and this goes also for male genitalic characters.

The workers of *Proceratium* are small to medium-small in size, generally ferruginous to reddish-brown in color, with greatly reduced eyes. The general habitus is distinctive (see Fig. 45) because of the under-turned gastric apex, which is a consequence

of the large, vaulted second segment of the gaster. The reduced apical segments bear a stout sting and are retractile to some extent within the second segment. The first gastric segment (postpetiole) is very variable in size with the species, and in some of the "*Sysphincta*" species it is reduced almost to the status of the myrmicine postpetiolar node (e.g., in *P. watasei*). In fact, these variations in the gastric proportions, and especially in the ratio of postpetiole to the succeeding segment, are of the type that must have led to the myrmicine gastric configuration from an ectatommine stock not far distant from *Proceratium* beginnings.

Most of the remaining characteristics of the genus are, like the reduced eyes and depigmented coloration, connected with the cryptobiotic life led by the species. The antennae are well developed, and their insertions have migrated anteromedially in order to give freer play to the funiculi straight ahead. The clypeus and "frontal" area are constricted by this migration of the antennal sockets, and the lobes of the frontal carinae are narrowed and tilted on edge so as not to hamper the movement of the scapes. The alitrunk is welded into one compact piece, with little or no trace left of the transverse dorsal sutures.

The antennae are 12-segmented in worker and female, and 13-segmented in the male. The maxillary palpi are 2-, 3-, or 4-segmented in the workers and females so far dissected, while in these same specimens, the labial palpi are either 2- or 3-segmented (known palpal formulae are 2,2; 3,2 and 4,3) [84].

Sculpture in the worker and female usually consists of fine, dense reticulo-punctuation, with sometimes a little superimposed rugulation, but in *stictum* the punctures are coarser and the entire sculpture rougher. The gaster is usually predominantly smooth and shining, with fine piligerous punctulation. The pilosity normally consists of abundant fine, short hairs, subappressed to inclined-erect, forming a kind of pile over large areas of trunk and appendages. Occasional longer fine hairs are more scattered. There is often a definite fine carina running down the middle of the cephalic dorsum, probably homologous to the similar feature of *Acanthoponera* and *Heteroponera*.

In the female, the compound eyes are much larger than the minute ones of the worker, and are similarly situated near the

middle of the sides of the head. The female and male often (particularly in the North American species) have the metanotum produced into an acute median tooth or bladelike carina.

The female may be either fully winged (and later dealate) as usual for ants, or she may appear in ergatoid form, intergrading to the worker form. Both normal and ergatoid females may occur in the same nest.

The wings in both sexes are a somewhat reduced version of the basic ponerine type; in those I have seen of *Proccratium*, the forewing vein (Rsf2+3) formed of the second and third free abscissae of the radial sector is missing, leaving a single large polygonal cubital cell; occasionally, the distal part of this vein, equivalent to Rsf3, is retained, as in some *Myrmica*. The cross-vein m-cu is often lacking, too.

Details of morphology are dealt with by Kennedy and Talbot (1939, all castes), by Kratochvíl (1944, all castes) and by M. R. Smith (1943, male) for different species. The larvae, at least during later stages of development, develop large, smooth bosses that are arranged symmetrically over the body and are unlike those of any other ant genus. However, the larvae are known for only the North American species, and even then from very few specimens (G. C. and J. Wheeler, 1952a: 134-137, pl. 5, figs. 17-27). The male genitalia are figured by Kennedy and Talbot (*loc. cit.*), but I can find no close correspondence between my dissections of males of the same species (*silaceum*) and their drawings of these organs. The genitalia need to be restudied.

Proccratium is widely distributed in the warmer half of the North Temperate Zone in areas with sufficient moisture in the soil, being found from Spain to Japan, and it ranges through southeastern Asia, the Malay Archipelago to New Guinea, reaching southeastern Queensland in Australia [96] and having a representative (*relictum*) in Fiji in the east. In eastern North America, three species range widely in the forested areas from the Gulf of Mexico northwards, two of them reaching New England and the Great Lakes region [97, 98]. Another three species range widely in southern Mexico and Central America, and one of these has been taken on Cuba, to which country it may have been historically introduced. In addition to the North African species,

which are part of the southern Palaearctic fauna, there are two species, *arnoldi* (Southern Rhodesia) and *toschii* (Kenya), known from the African Continent.

We have only fragmentary, and often contradictory, information on the biology of *Proceratium* species. The nests are small, usually consisting of from 10-50 workers and one dealate female, though sometimes supernumerary queens, either dealate or ergatoid, are present in one nest. The nest consists of small rounded chambers hollowed out of soft rotten wood or in the soil; toward the cooler limits of the range, particularly in North America, nests and foraging workers are found under deepset rocks instead of in rotten wood. The nest site is usually in forest shade, in old moist gardens, or similar habitats that are constantly moist.

In the artificial nest, *Proceratium* species have been offered various foods. Fiala (in Kratochvíl, 1944) states that his *mclinum* (= *fialai*) took bee honey; Haskins (1930) found that his *croceum* would not take honey, but that both adults and larvae would feed on the larvae, and sometimes on the pupae, of various genera of ants. Haskins also reported his *croceum* feeding on "meat" after long hesitation. L. G. and R. G. Wesson (1940) studied *pergandei* in Ohio, and noted that this species refused the brood of *Camponotus* and *Formica* as food, and also avoided all other insects offered, both living and dead. The *pergandei* did, however, appear to feed on the gastric contents of several *Formica* and *Camponotus* worker adults.

Observations made more recently by Wilson and myself and others (to be published elsewhere) on *silaceum* and *pergandei* indicate that these species may be specialized egg predators, eating the eggs of various other arthropods, especially of spiders. This may be the explanation also for the Wessons' observation of *pergandei* feeding on the gastric contents of dead worker ants, for these ants may well have been carrying eggs in their ovaries. Just how far egg predation extends as a general habit among *Proceratium* species is not known.

Males and females are produced in small numbers, usually toward the end of the summer in the North Temperate Zone, where the nuptial flight occurs normally during the last half of August in many places. The flight takes place during afternoon (*mclinum*), and both sexes climb to a distance from the nest

entrance before taking flight. Workers issue from the nest also during the nuptial flight, as is often the case with otherwise cryptobiotic ants. The flight has been observed by Fiala, (in Kratochvíl, 1944) for *melinum*.

Haskins (1930) mentions the curious habit in *croceum* workers of backing up to the brood of other ants to employ the sting. What, if any, function can be ascribed to this action is a matter for future observation to settle. The general activity of *Proceratium* species is rather sluggish, although they can move quickly on occasion. The antennae are held porrect in front of the head and during foraging are vibrated ceaselessly, much in the manner of cerapachyines and dorylines.

On the basis of external morphology, the species of *Proceratium* can be grouped conveniently in series from thick-noded ("Sysphincta") to "super-*Proceratium*" with a scalelike petiole. One can see seven vague groups:

Stictum Group: *stictum*. Pergandei Group: *algericum* [85], *mayri*, *pergandei*, *wataschi*. Melinum Group: *itoi*, *melinum* [94]. Micrommatum Group: *convexiceps*, *micrommatum*. Arnoldi Group: *arnoldi*, *toschii*. Silaceum Group: *carinifrons*, *croceum*, *japonicum*, *lombokense*, *longigaster*, *manicum*, *normandi*, *numidicum*, *papuanum*, *silaceum*. Relictum Group: *relictum*. Unassigned: *californicum*.

PROCERATIUM species

The species marked with an asterisk (*) have previously been placed in *Sysphincta* by most authors, although those names not marked "n. comb." were either placed in *Proceratium* when originally described, or were transferred to *Proceratium* by some author (Mayr, Dalla Torre) subsequently. The names marked "n. comb." were all originally described in *Sysphincta*.

- (?) *algericum* Forel, 1899b:305. * n. Africa [85]
- (T) *arnoldi* Forel, 1913a:210. * S. Rhodesia [86, Figs. 1, 34, 35]
- (?) *californicum* T. W. Cook, 1953:45. California [87]
- (P) *carinifrons* Menozzi, 1939:175. Sumatra, Philippines [88, 91]
- (T) *convexiceps* Borgmeier, 1957:120. Costa Rica [89]
- (P) *croceum* (Roger), 1860:288. se. N. America [Figs. 26, 31]
- (P) *itoi* (Forel), 1917:717. n. comb. * Japan [90]
- (P) *japonicum* Santschi, 1937:362. Japan

- (T) *lombokense* Emery, 1897b:593. Lombok [91]
longigaster Karawajew, 1935:59. Indo-China [88]
- (P) *mancum* Mann, 1922:6. C. America, s. Mexico [92]
- (P) *mayri* Forel, 1899b:306. * s. Europe [85]
- (P) *melinum* (Roger), 1860:291. * s. and e. Europe [94, 84, Figs. 24, 29]
- (P) = *europaea* Forel, 1886:elxiii. * n. syn.
 = *rossica* Arnoldi, 1930b:144. * n. syn.
- (T) = *fialai* Kratochvíl, 1944:54, 86. * n. syn.
- (P) *micrommatum* (Roger), 1863:176. * Panama, s. Mexico, Cuba [93, Fig. 28]
- (P) = *cavernicola* Borgmeier, 1937:221. * synonymy by Borgmeier, 1957:118.
- (?) *normandi* Santsehi, 1929a:138. n. Africa [95]
- (P) *numidicum* Santsehi, 1912a:172. n. Africa, Balkan Pen. [95]
- (T) *papuanum* Emery, 1897b:592. N. Guinea, ?e. Australia [96, Fig. 32]
- (T) = *Ponera caeca* Donisthorpe, 1949a:491. n. syn.
- (P) *pergandei* (Emery), 1895a:264. n. comb. * se. N. America [97, Fig. 23]
- (T) *relictum* Mann, 1921:413. Fiji. [Fig. 33]
- (P) *silaceum* Roger, 1863:172. se. N. America [98]
 = *crassicorne* Emery, *rugulosum* Wheeler and *vestitum* Emery, synonymy by Creighton, 1950:36-40.
- (T) *stictum* Brown sp. nov. n. Queensland [99, 84, Figs. 27, 45, 46]
- (T) *toschii* (Cousani), 1951:167. n. comb. * Kenya [100, Figs. 25, 30]
- (P) *watasei* (Wheeler), 1906:303. n. comb. * Japan

DISCOTHYREA Roger

- > *Discothyrea* Roger, 1863:176. Type: *Discothyrea testacea* Roger, 1863, monobasic.
- > *Pseudosysphincta* Arnold, 1916:161. Type: *Pseudosysphincta poweri* Arnold, 1916, by original designation, monobasic. n. syn.
- > *Prodiscothyrea* Wheeler, 1916:33. Type: *Prodiscothyrcra velutina* Wheeler, 1916, monobasic. n. syn.
- > *Pseudosphincta* Wheeler, 1922:645, 762. Variant spelling of *Pseudosysphincta*. n. syn.

The genus *Discothyrea* includes a modest number of small to minute species, very compact in form and extreme in the development of the "proceratiine traits," and especially notable for the exaggerated enlargement of the apical antennal segment. The raised median portion of the clypeus between the frontal lobes is fused with the frontal lobes and elevated with them to form, in some species, a flat-topped platform (Fig. 47, 48)

between the antennal insertions; in other species, the width of this structure is decreased, and finally, in several species, it is reduced to a simple vertical plate or flange that separates the now very closely approximated antennal insertions. The lower part of the clypeus is reduced to a strongly projecting apron covering the middle parts of the mandibles (Fig. 48) and serving as the front rim of the platform upon which the antennae are inserted. The clypeal apron may be rounded or truncate as seen from above.

With the enlargement of the apical antennal segment, the segments between it and the first funicular segment (pedicel) become axially compressed and tend to fuse one to another to reduce the number of segments. This fusion and reduction renders determination of segment numbers virtually impossible in some species, even when one uses cleared specimens under the higher powers of a compound microscope. Furthermore, it is clear that fusion is irregular in some species, and differs in degree among individuals, and even on different sides of the same specimen.

In spite of this difficulty, the antennal segmentation has been granted value as a generic character. *Discothyrea* has been considered to be "normally" nine-segmented, including the scape, although actually there are a number of species in Africa, the New World, and Australia with lesser counts: eight, seven, and even as few as six antennal segments, including the scape; for a discussion of this situation, see Borgmeier, 1954:191.

Prodiscothyrea is distinguished primarily on the basis of its ten-segmented antennae; the other characters of cephalic structure cited by Wheeler as diagnostic are all found well developed in one or more nine-segmented species of *Discothyrea* (e.g., *clavicornis*, *oculata*, *mixta*), and therefore are useless as generic characters. We therefore have the anomalous situation in which one genus is distinguished by its having ten antennal segments, from another genus that has six, seven, eight, or nine. Clearly, the ten-segmented species belong in *Discothyrea*. But the same character does not rest its variation at ten segments, for the new species *mixta* [105], otherwise exceedingly similar to certain *Discothyrea* and *Prodiscothyrea* species, turns out to have eleven

segments. And there is *Pseudosysphincta poweri* to be considered; essentially, this last is a *Discothyrea*, but with twelve antennal segments. Now that we have an unbroken series of species with all possible segmentations from six to twelve, it is plainly not advantageous to recognize more than one genus for this group, at least until some better character can be found on which to base the separation. Except for the segmentation, *Discothyrea* in this new, collective sense is an exceptionally homogeneous and well-marked genus.

Some other characters of the *Discothyrea* worker may be reviewed. Eyes small to minute, placed near or anterior to the middle of the sides of the head. Mandibles rather small, apex acute, followed by a usually edentate masticatory margin that is straight to concave and lined with a very even, close rank of minute peg-like bristles; the masticatory border is terminated basally by a rounded or bluntly toothlike basal angle. The palpi of maxilla and labium are variously segmented, according to species; Wheeler (1916:33 and pl. 4, fig. 3) found a formula of 4,4 in *velutina*, whereas Borgmeier counted 1,3 in *sexarticulata* (1954:193, figs. 8, 9). A comparative study of the maxillary palpi, very difficult in these small insects, remains to be made by the first reviser of the genus. (But see the recent study by Borgmeier, 1957:122-125.) The mouthparts are altogether peculiar in their reduction, and it would be interesting to know what the food is.

The alitrunk is short, usually vaulted and sutureless dorsally, and terminates posteriorly in a declivity that is more or less distinctly set off from the dorsal surface by paired propodeal angles or vestigial teeth. Petiole reduced, anteroposteriorly compressed and not very high, usually in the form of a thick disc or scale, bluntly pointed above or with one or two low rims running around its free margin from one side to the other. The node is normally attached over a large proportion of its posterior surface to the postpetiole. Postpetiole and succeeding gastric segments are arranged much as in *Proceratium* (Fig. 47). Legs stout; spur of posterior leg pectinate, spur of middle leg very small, perhaps absent in some species. Tarsal claws small, simple.

Basic sculpture consisting of minute piligerous or tuberculate punctures, in most species crowded densely over most of the

body, rendering it opaque or subopaque; rarely, however, the punctures are much smaller, spaced, and the surface generally shining. Usually, the sculpture tends to thin out more toward the gastric apex, so that shining interspaces appear in the species with this type of sculpture. Entire, or nearly the entire, body covered by a very dense, fine erect pubescence or pile, helping to render the surface more opaque, or else the pubescence reduced to virtually invisible pruinescence. Longer hairs are scarce or absent. Integument color ranges from testaceous to dark brown or mahogany, or combinations of these.

The female is like the worker, but slightly to distinctly larger; usually with well developed ocelli and flight sclerites of the thorax, and with larger compound eyes. Ergatoid females may occur in some species, as workerlike individuals with rather large compound eyes and a trace of one or more alitruncal sutures remaining on the dorsum. Wing venation is of the *Myrmecina* type (see M. R. Smith, 1943: fig. 5C), with Rs+M, Rsf2+3, and Rsf 4+5 lined up to form a single strong unit joining the anterior margin of the wing near its apex (i.e., "radial cell closed"). Mf2 is present, but not r-m, Mf3 or beyond, or m-cu. Of course, wings are known for only a few of the species so far.

The male is smaller and more slender than the female, with a subglobose head, large compound eyes, small ocelli, and well developed, triangular mandibles shaped much as in the worker. Antennal insertions very close together, separated by a vertical carina representing the fused clypeus and frontal lobes in the female castes; a more or less distinct vestige of the horizontal clypeal apron is also present. The antennae are composed of a short scape, approximately equalling in length the succeeding three segments, and twelve funicular segments, all but the first of which (pedicel) are longer than broad. The first segment of the funiculus is globular or subglobular and broader than long to slightly longer than broad, according to species. The funiculus as a whole is slender, with slight incrassation toward the apex.

Mesonotum with or without notauli. Wings as in the female. Petiole as in female, but usually longer and lower. Gaster variable in shape and proportions, the postpetiole either larger than or smaller than the succeeding segment; apical segments only slightly deflected ventrad. Sculpture of fore part of body much

as in the corresponding workers, densely punctulate, in the species so far known; gaster more smooth and shining. Color dark brown or black. Genitalia as yet remaining unstudied; hypopygial border rounded.

Larva remaining undescribed.

The range of *Discothyrea* lies predominantly within the tropics and warm temperate parts of the Southern Hemisphere, although we have records for the southeastern United States and for Hainan Island, southern China, and Formosa. The genus is represented by one (and possibly more) species on New Caledonia, one on New Zealand, two or three in the southern Brazil-northern Argentina area, and two or so in South Africa. It is restricted to the moister nest sites, though it can be carried about by commerce in plant roots and humus, and therefore often turns up in gardens. It should be expected in greenhouses and plant propagating beds wherever the temperature and moisture are held sufficiently high. Considering the relative abundance of colonies as measured by number of collections to date, it seems that by and large, *Proceratium* and *Discothyrea* tend to have complementary distributions outside the tropics.

Due to its chiefly tropical and south temperate distribution, as well as to its small size, inconspicuous nests, death-feigning habits and cryptobiotic tendencies, *Discothyrea* is relatively rarely collected, and little is known concerning its habits. Nests are found in rotten wood, rotting nuts, etc., in the leaf litter, and in large rotting logs. In the hilly parts of southeastern Australia, I have found them under stones rather frequently, especially in the galleries of other species of ants. Individual workers have been recovered from plant roots and similar situations in the soil, and in moss covering logs and rocks in wet areas. It is probable that the colonies are more frequent than they seem to be to a collector working in the usual way to search for ants.

The food is unknown; from the aberrant nature of the mouthparts, it must be something rather special. Several authors have thought that it "is almost a certainty that they are carnivorous," and Moore (1940:308) gave it as his opinion that the food of *Discothyrea* in New Zealand might consist of mites taken in ant nests. Since the similarly specialized *Proceratium* is now

thought to be an arthropod egg predator, in part at least, a similar feeding habit could possibly be followed by *Discothyrea*; at any rate, it is worth checking in the field. Colonies of *Discothyrea* thus far examined held ten or twenty workers plus a female and brood; winged forms can be produced in equal or even greater numbers, and both sexes are normally produced in the same nest.

DISCOTHYREA species

New combinations are marked with an asterisk (*). *D. bryanti* and *D. velutina* are transferred from *Prodiscothyrea*, *D. poweri* from *Pseudosysphincta*.

- (P) *antarctica* Emery, 1895a:266. N. Zealand: North I.
- (T) *bidens* Clark, 1928:38. Australia: s. e. Victoria [101]
- (T) *bryanti* (Wheeler), 1917:29. * Malaya, Java, Hainan I.
- (P) *clavicornis* Emery, 1897b:593. Melanesia
- (T) *crassicornis* Clark, 1926:46. sw. Australia [101]
- denticulata* Weber, 1939:100. British Guiana [103]
- (P) *globus* Forel, 1905:4. Java
- (?) *hewitti* Arnold, 1916:160. S. Africa [102]
- horni* Menozzi, 1927:270. Costa Rica [103]
- humilis* Weber, 1939:100. Panama [103]
- icta* Weber, 1939:101. Trinidad [103]
- (?) *isthmica* Weber, 1940:78. Panama [103]
- (T) *lae* Clark, 1934a:29. S. Australia: Lofly Range [101]
- (T) *mixta* Brown, sp. nov. Liberia [105, Figs. 47, 48]
- (P) *ncotropica* Bruch, 1919:400. [103]
- (P) *oculata* Emery, 1901:52. w. and e. Africa [102]
- (?) *patrizii* Weber (emended from "patrizii"), 1949:2. [102]
- poweri* (Arnold), 1916:162. * S. Rhodesia [102]
- (T) *remingtoni* Brown, 1948b:38. N. Caledonia [104]
- sauteri* Forel, 1912:47. n. status Formosa
- (?) *sculptor* Santschi, 1913:302. n. status French Congo [102]
- (T) *sexarticulata* Borgmeier, 1954:191. Brazil: S. Cat., S. Paulo [103]
- (P) *testacea* Roger, 1863:177. se. United States [103]
- (P) *traegaardhi* Santschi, 1914:3. w., e., s. Africa [102]
- (T) *turtoni* Clark, 1934b:53. Australia: Victoria [101]
- (T) *velutina* (Wheeler), 1916:34. * n. Queensland

APPENDIX

The pages of this appendix are reserved for notes and descriptions dealing chiefly with species-level taxonomy and biology. In the descriptions, the abbreviations for measurements and indices are as follows: TL, total outstretched length of head and body, including mandibles. In ectatommines, many species have recurved gasters, and in these, the length measurement is made to the posteriormost point of the gaster in its normal position, this point usually falling on the curved tergital surface of the vaulted second gastric segment. HL, maximum measurable length of head, including clypeus but not mandibles, as seen from full-face (dorsal) view. The occipital angles are normally included if these project. HW, maximum measurable width of head as seen from full-face view, eyes are usually excluded. CI, or cephalic index, is $HW/HL \times 100$.

In cases where places of deposition, often cited in brackets, are abbreviated, [MCZ] stands for the Museum of Comparative Zoology at Harvard College, Cambridge, Massachusetts; [USNM] stands for the United States National Museum at Washington; [CAS] stands for the California Academy of Sciences, San Francisco; [NM Vienna] stands for the Naturhistorisches Museum at Vienna.

[1] ACANTHOPONERA PERUVIANA sp. nov.

(Figures 6, 7)

Holotype worker: TL 8.7, HL 1.73, HW excluding eyes 1.56 (CI 90), greatest diameter of eye 0.43, scape L 1.07, WL 2.60 mm.

Similar to *A. mucronata*, but differing as follows: Head with sides more nearly straight and parallel, occipital angles rectangular. Eyes larger. Sculpture of head looser, with wider, more shining spaces between the rugae, especially along both sides of median carina and in antennal scrobes. Propodeal spines heavier and longer, approaching 0.7 mm. in L (ca. 0.4-0.5 mm. in *mucronata* workers), gently divergent; when viewed from the side, more definitely arched in their basal halves and less strongly elevated than in *mucronata*.

Shape of petiole shown in Figure 7; note the continuous curve formed by anterior nodal face and dorsal outline of spine. Gaster markedly depressed and somewhat broadened (Fig. 6), with a deep constriction between postpetiole and second segment, the latter slightly broader and with a conspicuous posterior impression extending forward into the main tergital surface from the depressed apical band. Second segment only feebly down-curved, and the exposed sternum correspondingly longer than in *mucronata*. Apical segments retracted in this specimen, but the slender sting exerted.

Gastric sculpture much coarser, denser and more opaque than in *mucronata*, consisting of abundant, uneven-sized punctures, slightly larger on the postpetiole than on the second segment, forming a dense irregular rugoreticulum on the sides, less dense in the middle, where narrow, shining interspaces exist on the second segment.

Erect hairs abundant, though fewer than in *mucronata*, but thicker, stiffer and longer. Body color bright ferruginous yellow.

Holotype a unique worker [CAS] from Monson Valley, Tingo Maria, Peru, October 26, 1954 (E. S. Ross and E. I. Schlinger leg.).

[2] ACANTHOPONERA CRASSA sp. nov.
(Figure 10)

Holotype worker: TL 6.2, HL 1.24, HW excluding eyes 1.07 (CI 86), greatest diameter of eye 0.30, scape L 0.85, WL 1.82 mm.

Similar to *A. minor*, but a little larger. Head narrowing from a point in front of eyes toward occiput, narrowest, and sides sloping inward, behind eyes near the much-rounded occipital corners; occipital margin short, median section straight, or even feebly convex. Median pronotal eminence low, but better developed than in other species of the genus. Metanotal groove distinct, broad and rather deep. Propodeal spines (L ca. 0.35 mm.) straight and obliquely elevated as seen from the side; diverging, with tips feebly curved mesad as seen from above. Petiolar node (Fig. 10) thicker than in *minor* (Fig. 9), its posterapical tooth deflected more or less dorsad. Gaster very much like that of *minor* (Fig. 4) in general form, but slightly larger.

Sculpture in general a little coarser on head, alitrunk and node than in *minor*, the interspaces larger and shining. Pronotal rugules forming a V around the median eminence. Gaster smooth, shining, with abundant fine, separated punctulae, giving rise to dense, reclinate golden-brown pubescence. Longer fine erect hairs abundant.

Body color orange-brown, legs more yellowish.

Holotype [CAS] one of a series of 4 workers taken 6 miles west of Santo Domingo de los Colorados, Pichincha, Ecuador, February 23, 1955 (E. S. Ross and E. I. Schlinger leg.). The remaining three workers are paratypes [CAS, MCZ]. HL 1.22-1.25 mm., CI 87-89.

Considered as belonging to *A. crassa* is a short series of workers [USNM, MCZ] from Hamburg Farm, Santa Clara Prov., Costa Rica, February 26, 1925 (F. Nevermann leg.). The MCZ specimen measures HL 1.19, HW excluding eyes 1.03 mm. (CI 87). The color is much lighter than in the type series, being bright ferruginous yellow, and the occipital angles are somewhat more abruptly rounded; transverse part of occipital border broader than in type, concave in middle. Eyes a little larger, propodeal teeth shorter and feebly bent in side view, and the posterapical petiolar teeth flattened and only slightly deflected dorsad.

In color and head shape, the Costa Rican samples are somewhat intermediate, tending toward *minor*, but in the characters of total size, metanotal groove and petiolar thickness and form, they are clearly related to *crassa*. The differences from *minor* could possibly represent geographical variation, but the known distribution of *minor* and *crassa* does not support this very well.

[3] The taxonomy of the New World *Heteroponera*, like that of *Acanthoponera*, remains in a very unsatisfactory state, due primarily to the lack of sufficient material and to the inadequacy of some of the descriptions of forms undoubtedly belonging here. There are a few firm points, however. There is not much doubt about what *dolo* is; Roger's description fits reasonably well this large, yellowish species, the commonest one in collections, and distributed widely from Rio de Janeiro south to Uruguay and Misiones (the westward extent of its range is unknown). I have

seen quite a few series and strays from within this area, and the species is reasonably constant: the worker head length (HL) runs from about 1.20 to about 1.50 mm., and the cephalic index from 85 to 91. The occiput seen full-face is slightly concave in outline. Judging from the original description, Forel's var. *aurea* is apparently a semicallow worker of *dolo*.

H. carinifrons is a distinct species, easily recognized by its small size, blackish color and unarmed node; it is now known from various localities in Chile, and the variation from one series to the next is slight. *H. microps* Borgmeier is very small, has minute eyes and an unarmed, rather scale-like petiolar node, and is light ferruginous in color. In addition to the types, from southeastern Brazil, I have seen specimens of *microps* taken at Venecia, near Medellin, Colombia (S. Flanders leg.), a rather surprising extension of the range. The Colombian sample was taken near a sample of *Typhlomyrmex pusillus* Emery in the soil; *T. pusillus* is also an ant usually thought of as having a much more southerly distribution in South America.

With the *dentinodis* complex, we come to the serious confusion in *Heteroponera*. Up to now, there have been named in this group *dentinodis* itself, plus three varieties: *panamensis*, *inermis* and *schwebeli*. Mayr described *dentinodis* from southern Brazilian examples with a short tooth on the posterior apex of the node in larger workers, but said that this tooth was obsolete on the nodes of smaller workers. However, there is no definite statement that Mayr's large and small workers come from the same nest series, so we cannot be sure that they represent the same species. The few specimens I have seen from the southern part of Brazil are strays, and so we still have no assurance that the two types of workers represented in collections are conspecific, though this does seem likely. Emery complicated the situation by describing var. *inermis* from a female without developed posterapical nodal tooth; this female indicates either that the tooth character does not vary in correlation with size (i.e., is not markedly allometric, as Mayr implied), or, more likely, that another species exists with poorly developed tooth in all sizes of workers and females as well. We now know, in fact, that such a species exists in Lüderwaldt's var. *schwebeli*, but *schwebeli* seems too large to be the same as *inermis*. It may be that Emery's measurement was too low, but we shall not be sure of the identity of *inermis* until the type can be reviewed.

Referred to *dentinodis* provisionally are the following: a larger worker from Parecy Novo, Rio Grande do Sul; HL 1.02, HW without eyes 0.90, WL 1.35 mm., CI 88. One smaller worker each from Nova Teutonia, Santa Catarina (F. Plaumann leg.), and Agudos, S. Paulo (W. W. Kempf leg.), measure HL 0.78-0.79, HW 0.70-0.71, WL in both examples 1.04 mm.; a winged female from Petropolis, Rio de Janeiro (Coll. Borgmeier): HL 0.97, HW 0.85, WL 1.32, forewing L about 3.5 mm. The cephalic index for these three large and small workers and one female ranges from 88 to 90. The female has a well developed and acute posterapical nodal tooth. An anteroposteriorly compressed node is characteristic for all of these specimens.

The holotype of var. *schwebeli*, from Estação Alto da Serra, S. Paulo, has HL 1.12, HW 0.92, WL 1.51 mm.; CI 82. A similar, but slightly smaller specimen from Jaguara, Paraná, in Coll. Borgmeier, has HL 0.98, HW 0.78, WL 1.21 mm.; CI 78. Both of these, as well as a dealate female from S. Teresa, Espirito Santo (O. Conde leg.), have dense, irregularly punctate sculpture, opaque for the most part; interpunctural spaces of postpetiole narrow and finely reticulate or coriaceous. A similar specimen from Agudos, S. Paulo (R. Müller leg.), Coll. Kempf, measures HL 1.07, HW 0.87, WL 1.43 mm.; CI 81. This last example is more shining, especially on the gaster, where the interpunctural spaces are largely smooth and shining on postpetiole as well as on the succeeding segment. So far as I can see, *schwebeli* is distinct from the sympatric *dentinodis* in shape of petiolar node (see key) as well as in the narrower head. The female node, however, is more anteroposteriorly compressed than in the worker. Total size averages larger than in the few *dentinodis* I have seen, but worker size even here overlaps slightly. For the time being, it seems best to recognize *schwebeli* as a species in its own right, though it may later prove to be the same as *inermis*, as mentioned above.

Two workers in the Borgmeier Collection (Nr. JBV 47) from Campinas, Goiás, Brazil, resemble large *dentinodis* in size and general appearance, but are light yellowish-ferruginous in color and have thicker nodes (not as thick from front to rear as in worker *schwebeli*, however) with the posterior apex continued backward as a stout subconical projection or tooth. Whether these

specimens represent a different species, or mere geographical variation in *dentinodis*, cannot be decided without material from intervening areas in Brazil.

Concerning var. *panamensis*, I have asked some questions about the type in the British Museum, kindly answered by Mr. G. E. J. Nixon, who made comparison for me with a paratype worker of the species I describe below as *H. inca* sp. nov. Mr. Nixon's remarks are adapted in part and follow in the next three paragraphs.

H. panamensis type is slightly smaller than *inca*, and more slender. Outstretched length (the small apical gastric segments are hidden and not included in length) of *panamensis* type about 3.8 mm. Color virtually the same as in *inca*. Head distinctly longer than broad and decidedly narrower than in *inca*, less convex dorsally and without the occipital lobes of *inca*; occipital margin straight.

Propodeal teeth very short, forming angular projections not longer than wide at base. The second gastric segment is much less strongly differentiated from the first than in *inca*, and is nearly the same width as the first segment (postpetiole). Left mandible with 7 teeth, the seventh tooth forming the basal angle; the three teeth next to the seventh tooth very weak.

Sculpture much finer than in *inca*; surface of head between the frontal area and occiput and between the scrobes quite dull, very finely longitudinally striate and with the median carina in full relief. Between scrobes and eyes the surface finely rugose, not easily defined at 40 \times ; toward the occipital angles the sculpture thickens slightly.

From this characterization, it appears that *panamensis* is much closer to *dentinodis* than to *inca*, and it is not impossible that *panamensis* and *dentinodis* are synonymous. However, the distributional facts and the darker color of *panamensis* are, it seems to me, sufficient cause to hold up synonymy until a direct comparison of the type with other material can be made. For the time being, *panamensis* is raised to nominal species status.

HETEROPONERA INCA sp. nov.

(Figures 12, 13)

Holotype worker: TL to apex of second gastric segment 4.8, HL 1.14, HW including eyes 1.10, HW excluding eyes 1.06 (CI

93), exposed scape L 0.76, greatest diameter of compound eye 0.24, WL 1.44 mm.

General habitus that of *H. dentinodis*, but more robust in build, darker in color, with a differently shaped head, longer propodeal teeth, thick petiolar node with calcarate ventral process, and with a proportionately larger postpetiole.

Head in full-face view as in Figure 12; note especially the somewhat depressed and lobiform occipital angles. Seen from the side, head strongly convex across vertex and central occiput; occipital lobes auriculate, broad, obliquely subtruncate, with narrowly rounded corners above and below, much as in *Gnamptogenys costata* and *G. menadensis*. Antennal scrobes weakly defined curving above the eyes and terminating indefinitely some distance behind toward the occipital angles. Eyes strongly convex, each with a circummarginal sulcus. Mandibles triangular, basal angles blunt; apical tooth and a smaller preapical tooth strong, acute, remainder of margin with coarse, shallow crenulation. Clypeus convex in the middle and with narrow, depressed anterior apron, the margin of which is feebly convex seen in outline from dorsal view. Scaopes short, incrassate toward apices; when laid straight back or nearly so from their insertions, falling slightly short of the occipital margin. Funiculi gradually thickened toward their apices; the last three segments could be considered as forming an indistinct club; penultimate and antepenultimate segments about as long as thick, segments II-VIII thicker than long.

Alitrunk robust, pronotum rounded above, separated from the narrower mesonotum by a deep-cut (possibly mobile) suture; inferior pronotal margin obtusely angled on each side. Mesonotum forming a single gentle convexity with propodeal dorsum; metanotal groove marked by a very indistinct transverse line or sulcus. Propodeal teeth well developed and acute, larger than in any other *Heteroponera* so far described; seen from above divergent, slightly longer than the distance between the inner sides of their bases. Petiole as in Figure 13; seen from above, the node is slightly broader than long, excluding posterapical tooth, which in this view is broad at the base, tapering to a narrowly rounded point.

Postpetiole large, semiglobose, broader than long, slightly narrowed around its apical border. Succeeding segment as long as postpetiole, but narrower (about as broad as long seen from above), weakly downcurved and tapering toward apex. Apical segments tapered rapidly apicad, at least partially retractile. Legs robust; each middle and posterior tibia with a single large pectinate spur; all tarsal claws slender and simple (without submedian teeth or denticles).

Mandibles smooth and shining (when clean), with scattered punctures. Antennae, gula, gastric apex and legs with very fine indistinct punctulation or reticulation, subopaque to opaque. Head, alitrunk, node and gaster irregularly reticulo-rugulose over an extremely fine microsculpture, opaque, with inconspicuous coarse punctures crowded on head and alitrunk, but becoming fewer and still less conspicuous posteriorly. Upper scrobes with fine transverse rugulae.

Normally exposed surfaces of body covered with an abundant and mostly decumbent, fine, light-colored pubescence, sparse only on the mandibles, gula and retractile segments of gaster. Body and appendages also with an abundant pilosity of fine, tapered erect hairs, uneven in length, the longest about twice the length of the propodeal teeth. Body color deep brownish-red, legs more reddish.

Holotype, one of a long series of workers taken about 6 miles west of Cali, Valle, Colombia, at an altitude of 1630 m., March 20, 1955 (E. I. Schlinger and E. S. Ross leg.), deposited in California Academy of Sciences. The paratypes have the same data as the type. TL 4.7-5.0, HL 1.11-1.20, HW 1.00-1.11, CI 91-93. Propodeal teeth vary slightly in length and thickness, but in general are longer than broad at base. Posterapical tooth of petiolar node varies considerably in length, sometimes being markedly shorter than as shown in Figure 13, and sometimes more slender and acute, but not much longer. Color ranging from that of the holotype to very dark reddish-brown. Paratypes in CAS, Coll. Borgmeier, USNM, MCZ.

[4] *Hcteroponera imbellis* (Emery). This little species is widespread in eastern, southeastern and southwestern Australia, where it makes small nests under stones or woody fragments, or

directly in the soil without cover. It forages at least partly during the daytime, and solitary workers can be seen leaving the tiny, inconspicuous nest entrance to move slowly about in the open and among the leaves and debris of the soil cover. Although Wheeler (1934, p. 140) thought it hypogaecic in habits, I have not found it so. One worker was seen carrying unidentifiable remains of a very small insect into the nest.

H. imbellis does not seem to be very conspicuous anywhere, but it is not rare. I have found as many as four nests in a single day's collecting at one locality. One nest contained over 70 workers and several ergatoid females. The ecological tolerance of this ant is surprisingly wide; it occurs in a great variety of vegetation zones, from the wet mountain forest of the Australian Alps (at least to 1300 m. altitude) and southeastern Queensland to dry savannah woodland in the southern Flinders Ranges of South Australia (Mt. Remarkable) and the treeless savannah west of Melbourne.

Considerable variation is seen in size, color, sculpture, length and abundance of pilosity, angularity of propodeum, and antero-posterior thickness of the petiolar node. A large part of the color variation is due merely to the long period of adult tenacity, which may cause whole broods of workers to appear very different from one nest to another. The color also affects the visibility of sculptural patterns. I have examined 21 nest samples, mostly in good series, from nearly as many scattered localities, including 6 cotypes of *occidentalis* and a type of var. *scabra*, and I believe that the forms listed in the synonymy can be defended at best only as local or nest variants of *imbellis*. All of the characters mentioned appear in varying combinations and degrees, and I find considerable intergradation connecting all series. The present material shows no obvious "racial" pattern on a broad geographical scale, even for single characters.

[5] Cotypes of *H. brouni* from the Canterbury Museum at Christchurch, N. Z., received through the kindness of Dr. R. R. Forster, were compared directly with the type series of subsp. *kiriki* and found to be as closely identical as series from two different nests can be. Wheeler's diagnosis of *kiriki* is not as representative as Forel's. I have followed Wheeler in recognizing

the obvious lapsus or typographical error in Forel's original spelling, "*brownii*," and in emending the name to *brouni*. The species is widely distributed in the North Island of New Zealand, but I have seen no specimens from the South Island.

[6] Justification of new synonymy and other systematic changes in *Rhytidoponera* attributed to Dr. E. O. Wilson are included in the manuscript he is preparing on the Ponerinae of Melanesia, amounting to a revision of the species of this region. Wilson collected extensively in Melanesia during 1954-1955, and on his return to the United States, he was able to make critical comparisons of MCZ material, including specimens forwarded to him out of his own Melanesian samples, with types in several of the principal European collections. This type-comparison work was important in establishing many of the new synonymies put forward here, both in his name and in my own.

[7] The *impressa* group, *R. aspera* and *R. croesus* were revised by Brown (1954b:1-11) and a number of names put into synonymy under these species. I have omitted these junior synonyms from the list.

[8] In his revision of the larger Australian *Rhytidoponera*, Clark (1936) placed a number of names proposed by earlier authors in the synonymy. Unfortunately, he failed to offer evidence for most of the synonymies, and it is possible that some of them are incorrect. In any case, they should all be reviewed. However, a spot check convinces me that most of his assignments in synonymy are probably correct. None of the synonyms from the 1936 work will be listed here.

[9] A previous guess (Brown 1952b:137) that *laevior* Stitz was based on part of the type series of *aciculata* (Fred. Smith) is strongly backed by an obscure reference of Roger (1860:307) that I had not noticed before. Roger here cites *aciculata* material in the Berlin Museum that was sent by Smith. There can be little doubt that this is part of the material used by Stitz to describe *laevior*. In order to clear up any doubt about this

synonymy, I here select Hunter River, New South Wales, as the type locality for *laevior*, since this is also the type locality cited by Smith for *aciculata*.

[10] *R. scaberrima* and *R. malandensis*, described from northern Queensland localities very close together, cannot be distinguished. Although *malandensis* was described as a subspecies of *R. laciniosa* Viehmeyer, from New Guinea, *laciniosa* clearly is not closely related to the Queensland form.

[11] I found this little species (*borealis*) fairly common everywhere in the open tall eucalypt woodland southeast of Darwin, at Berrimah, at Howard Springs, and along the edges of the Howard River gallery forest, in the Northern Territory of Australia. Foraging workers are often found abroad in bright sunlight. Nests are made directly in the soil, or under logs, at least during the dry season. I also have a worker from the Finnis R., N. T. (R. Parkinson leg.). Clark's description of *brunnea*, while failing to mention some details of sculpture, nevertheless fits this species passably well. It is the common representative of the *metallica* group in the Darwin area.

[12] *R. anceps* has been poorly known, due chiefly to its rarity and local distribution. Wilson has compared specimens from near Brisbane (W. M. Wheeler leg.) with Emery's type in Genoa, and he finds that they match well. In the Museum of Comparative Zoology are other samples from Tamborine Mt. (A. M. Lea) and National Park (H. Hacker), both localities also in southeastern Queensland near the New South Wales border. Very likely the species occurs in northeastern New South Wales. The most obvious character, and one Emery does not properly emphasize, is the very low, blocky petiolar node of the worker and female. Seen from the side, the worker node averages just about as long as high without the ventral process, the proportions varying slightly either way in different specimens. As seen from above, the node is as long as broad, or very nearly so. The dorsal surface is distinct, even subtruncate set off, but is always slightly convex and usually rises slightly from front to rear. The posterior face is vertical or slightly receding ventrad. The

head is not quite so wide behind as in related *metallica*-complex forms, and there is a weak impression in the middle occipital region, best seen when the head is tilted slightly back from full-face view. The scapes are rather slender and, when laid straight back, they surpass the occipital border by distinctly more than their greatest width. Funicular segments all more or less distinctly longer than broad. Color brown or reddish-brown, the gaster often darker brown, without metallescence. Second gastric segment finely striate in a transverse arch, which passes posteriorly into a longitudinal, concentric ellipse; this posterior region somewhat more shining.

In addition to the Queensland samples, I have two workers and a headless male that I provisionally call *anceps*, collected at the Thomas River Station, east of Esperance, Western Australia, by E. O. Wilson and C. P. Haskins. The locality is a wooded depression in the heath-covered sandplain, the trees being mainly paperbark (*McAlcaluca cuticularis*), yate (*Eucalyptus cornuta*) and wattles (phyllodineous *Acacia* spp.), the last-named contributing in places to the shrubby undergrowth. Thin leaf litter exists in some parts of the depression, but in the summer this is very dry.

The two workers apparently represent a rather dense population, for Wilson's notes mention, in addition to an abundance of *R. metallica* nesting in the ground, a smaller, "more slender" species, also nesting in the earth and foraging on trees and shrubs, especially at night, at the Thomas River locality. The specimens resemble the Queensland *anceps* very closely in all respects, except that the petiolar node is not quite so long. In dorsal view, the node is distinctly wider than long, but it is still much longer and lower than the nodes of *inornata* and *metallica*. In general habitus without magnification, the Thomas River *anceps* looks much like *inornata*, and probably acts like that species in the way it accompanies *metallica* in a restricted, relatively favorable habitat. If this Thomas River population is actually conspecific with *anceps* from Queensland, or even if the two populations represent very closely related but distinct siblings, as their external morphology suggests, their present distribution is a remarkable example of a relict peripheral persistence.

[13] *R. convexa* and *R. violacea* are very closely related, the best difference so far seen being the metallic green-violet surface reflections of *violacea*, lacking in its eastern twin. The ranges of the two forms appear to be separated by a broad gap in central Australia; neither has been found in the Northern Territory, despite intensive collection by G. F. Hill and others, including myself. *R. violacea*, widespread in Western Australia, has been taken along the Transcontinental Railway in that state as far east as Kalgoorlie (Wilson leg.) and even 1072 Mile Siding (Brown leg.), but it apparently does not cross the Nullarbor Plain. *R. convexa* ranges widely in eastern Queensland, and has isolated populations in the moister parts of the Flinders Ranges of South Australia [19], but its western limits are yet to be determined. The species separation is maintained here arbitrarily in the absence of decisive information concerning their status relative to each other.

The form described as *opacior* by Crawley is only a variant of *violacea* in which the metallescence is more obscure than usual, the green component especially being suppressed. Such individuals have been taken from the same nest series as some with the more usual violet-green coloration, e.g., in a nest series from Pioneer Siding, north of Norseman, W. A. (Brown leg.).

R. rufescens, heretofore placed as a variety or race of *convexa*, is really a good species, distinct in its more widely-spaced punctuation, as well as in the shape of its node, which averages wider at the base. The color is yellowish-ferruginous in *rufescens* specimens from Townsville (type locality by present selection), but a sample from Bowen, Queensland (F. H. Taylor leg.) is reddish-brown, approaching the hue of lighter *convexa* workers. I have true *convexa* workers also labelled as from Townsville (W. M. Wheeler leg.), but there is no sign of intergradation between the two forms in this region.

[14] *R. inornata*, described by Crawley as a variety of *metallica*, is clearly a species apart, restricted to the extreme southwestern strip of Western Australia and certain of the islands off Fremantle. On the eastern side, it reaches the Darling Range in back of Perth, where it overlaps *R. metallica* without producing intergrades so far as known. *R. metallica* appears to be scarce

in the main part of the *inornata* distribution, so that the two species approximately replace each other. Workers of *inornata* vary in color from light tan to blackish-piceous, the alitrunk usually being a trifle lighter than head and gaster; metallescence is lacking. The striation of the postpetiole is coarser than in Western Australian *metallica*, with broader interspaces, and is usually strongly arched over a small median area of more or less longitudinal rugulosity situated near the slightly emarginate posterior border. Punctures on the gaster vary from strong and numerous to virtually completely obsolete.

The sculpture of the second postpetiolar (second gastric) segment is arched rather strongly, and the raised costulae are separated by shining interspaces, whereas the sculpture of this segment in *metallica* is very fine, dense and more or less sericeous.

A normal dealate female and winged males were taken November 3, 1931, at Margaret River, W. A. (W. M. Wheeler). This female differs from the worker in the ways usual for ponerine ants, and has well-developed ocelli, compound eyes, thoracic flight sclerites and wing stumps. Wheeler's name *carbonaria* applies to common variants well within the normal spread of *inornata*.

R. inornata combines several features of the two related species *tasmanicnsis* and *victoriae*, from eastern Australia, where they replace *metallica* in damp forests. This situation is interpreted as "character displacement" by Brown and Wilson, 1956.

[15] RHYTIDOPONERA KURANDENSIS sp. nov.

Holotype worker: A small species, to the naked eye resembling *R. tenuis*, or to a lesser extent *R. victoriae*. TL 4.3, HL 1.02, HW 0.84 mm. (CI 82), WL 1.38 mm. Head broad-oval, almost sub-circular in outline seen full-face; greatest width at or immediately behind compound eyes (excluding eyes themselves), slightly narrowed in front of eyes. Occipital angles gently rounded, occipital border convex, with a very slight flat or concave tendency in the very middle. Clypeus convex, rather strongly projecting and forming an obtusely rounded angle in the middle. Eyes large (ca. 0.21 mm. greatest diameter) and strongly convex, occupying roughly $\frac{1}{4}$ the sides of the head. Antennal scrobes

short and shallow, not extending backward past the eyes. Antennae slender; scape 1.04 mm. long from basal collar; when laid directly back, surpassing the occipital border by $\frac{1}{3}$ its length. Mandibles large, finely denticulate.

Alitrunk rather slender (more slender than in *tenuis*), convex in profile, with a feeble impression in the region of the metanotum. Propodeal dorsum and declivity forming one rather flat curve, sloping downward caudad. Petiole distinctly smaller than in *victoriae*, and slightly smaller than in *tenuis*, with a short but distinct pedicel in front; free part of node nearly as high as long, with steep anterior and posterior faces rounding into a convex dorsal face; ventral process forming an acute triangle. Node seen from above broader than long, semicircular in outline, with the curved surface anterior. Gaster a little more slender than in *victoriae* or *tenuis*, but the lengths of the postpetiole and succeeding segment are in about the same proportion (3:4) to each other.

Sculpture of head, alitrunk and petiolar node consisting chiefly of coarse, contiguous foveolae or punctures with shining bottoms. Ridges separating these foveolae form rugulae, longitudinal on the head, mixed in direction on pronotum, and finer, closer and transversely oriented on the posterior half of the alitruncal dorsum. In general, this sculpture is coarser and more shining than in *tenuis*, and it lacks the interspersed dense punctulation found over the alitrunk and node of *tenuis*. Postpetiole with loose, irregularly-spaced costulae arching over a median posterior area of indistinct, mostly obsolete costulae forming a concentric longitudinal fusiform pattern, with a few coarse, shallow elongate punctures; costular interpaces and much of the postero-median area nearly smooth and shining. Second gastric segment costulate on the same pattern as the postpetiole, but much more weakly and with wider, smoother interspaces; a large postero-median area completely smooth and shining, with scattered small punctures.

Erect hairs fairly abundant over most of body, mandibles, scapes and legs; similar in abundance and distribution to those of *victoriae*, but averaging a little shorter. Appressed hairs of gastric dorsum few and very small, inconspicuous, more scattered

than in *victoriae*, and about the same as or fewer than in *tenuis*. Color deep, more or less reddish brown; mandibles, antennae and legs lighter, more yellowish.

Holotype worker [MCZ] collected at Kuranda, near Cairns, northern Queensland (W. L. Brown leg.). Paratypes: 14 workers representing six or more nest series from Kuranda and immediate vicinity (W. M. Wheeler leg., October 19, 1915; Brown leg. October 29-30, November 1, 1950). Also, four workers labeled "Cairns dist." (F. P. Dodd leg.) which probably came originally from Kuranda, near Dodd's home. My collections were made in rotting logs in rain forest, and consist of strays rather than colonies, probably because I did not at the time distinguish between *kurandensis* and *victoriae*, one or both of which were common at the same site. The only full colony of *victoriae* I took here, however, was in a large, rotting polypore fungus growing from the earth of the forest floor. The *kurandensis* workers may have belonged to diffuse colonies living in the rotten wood, but my notes do not mention the discovery of any brood with them.

Variation within the paratype series is slight. All workers are close to the holotype in size and proportions; in some of them, the head is a little more nearly quadrate, owing to less convex sides and occiput. There is slight variation in the height and thickness, as well as the angularity, of the petiolar node as seen from the side, and different specimens differ slightly in the density and distinctness of the gastric sculpture. Color varies from light brown (tenerals?) to piceous. The appressed pubescence of the second gastric segment is at best very sparse and inconspicuous, and in some specimens can scarcely be made out even in the best lights and magnifications. Paratypes to be deposited in USNM, MCZ and one or more Australian collections.

[16] RHYTIDOPONERA CHINOOPYX sp. nov.

Holotype worker and two paratype workers: Like *kurandensis*, but with the entire exposed tergital surface of the second gastric segment densely and uniformly covered with fine, short appressed pubescence, directed posteriorly and mesad. This pubescence forms a distinct brownish-yellow cast over the segment, but does not quite conceal the sculpture beneath. The individual setae of

the pubescence arise from myriad fine, separated punctulae, but otherwise the sculpture is like that of *kurandensis*. *R. pulchella* Emery, of New Caledonia, is very different in other ways, but has somewhat similar dense pubescence on the gastric dorsum; however, in *pulchella* the pubescence is less fine and is more whitish in color.

Holotype and two paratype workers taken (apparently together) at Millaa Millaa, Atherton Tableland, northern Queensland, at an altitude of about 2500 feet, undoubtedly in rain forest (P. J. Darlington leg., April, 1932). Deposited in MCZ.

Except for the gastric pubescence, *kurandensis* and *chnoopyx* are so similar that they could represent the same species. I prefer to separate them specifically for the time being, since I feel that sibling species may be rather common in this limited Atherton Tableland-Cairns region. The similar, but longer-headed species *tenuis* and *peninsularis* [27] form a more or less parallel *Artenkreis*, and it is worth noting that no two of the four forms mentioned in this paragraph have ever been taken at exactly the same locality. *Rhytidoponera* of this general group are well worth further investigation in northern Queensland.

[17] The group of species related to *R. punctata* includes robust, medium-sized entities of black or brown color, very finely and evenly reticulo-punctulate over most of the body, so that the integumental surface is largely opaque. In addition, the head and alitrunk (especially) bear larger, conspicuous punctures or foveolae. These forms are distributed widely in the drier parts of South, central and southwestern Australia, but up to now, they have been only very sporadically collected, which is unfortunate for the taxonomy, seeing that there is a great deal of variation in sculptural and minor structural details from nest to nest and especially from place to place. As might be expected, there seem to be more names than there are species, in large part due to splitting by Clark and Crawley. I have not seen the types, or even topotypical material, of *R. punctata*, so I shall suggest no formal synonymy here. However, it does seem to me that *R. flindersi* is very likely to prove a synonym of *punctata*. And material referable to *punctata* from Forrest, Western Australia [C. Barrett leg., MCZ] and near Balladonia, W. A.

[E. O. Wilson and A. Douglas leg., MCZ] shows that *punctata* may be distributed widely, if sporadically, across the wastes at the head of the Great Australian Bight, or at least that the distance separating eastern and western populations of the complex is not so great as has generally been assumed. In Western Australia, the two forms *douglasi* (= *levior* Crawley) and *rufo-nigra* are very like *punctata*; in *douglasi* the conspicuous punctures are much smaller and farther apart; however, some specimens (e.g., from Dongara, W. A.) are difficult to assign, and may be intergradient. A close study should be made of these forms in the Perth area; if they are found to intergrade there, synonymy with each other and with *punctata* would seem fairly certain. However, it is also possible that character displacement is operating here.

The *punctata*-group representative in central Australia is *R. incisa*, of the MacDonnell Ranges, where it is fairly common in my experience. This form is the most distinct of the group, and seems to be well isolated from the other species; however, we must expect further members of this complex to turn up from ranges to the south of the MacDonnells, in South Australia, and these may well link *incisa* to *punctata* if they do occur.

[18] Wilson (MS. notes) has compared an MCZ specimen from Broken Hill, N. S. W. (F. W. Shepherd leg.) with types of *maniae* and *spatiata* in the Forel Collection. He finds that, "*maniae* is the same as *spatiata* — the types are nearly identical; *spatiata* is somewhat larger and with a proportionately broader head, but the Broken Hill specimen is intermediate in both characters." I have also found that the Broken Hill specimens (determined as *spatiata* by Clark) are very similar to some collected by Zietz, Tepper and myself in the Lofty Ranges east of Adelaide. The types of both species probably came also from this neighborhood, more precisely the dry eastern scarp of the Lofties, such as the locality, at Barren Falls, near Mannum, South Australia, where I found *maniae* avoiding the heat of the day in December, and foraging at the same time as *mayri* after late afternoon shadows fell on the canyon floor. *R. maniae* is essentially a species of the Murray-Darling drainage area. To the

north and west, in the Flinders Ranges, it is apparently replaced by another, similar species that I have not yet satisfactorily determined [19].

Wilson has called attention to the close similarity between *maniac* and *R. hilli* Crawley, from the north of the Northern Territory. The two are indeed similar, but *hilli* averages lighter in color. The *hilli* types (Stapleton, N. T.) are brown with reddish gaster, while a series I took at the Mataranka Hot Spring, on the Roper River, is a rather uniform rich orange-brown. In these two series, the second gastric segment is usually transversely striolate, but occasional examples have the posterior part with longitudinally or obliquely arched striolation approaching the condition in *maniac*. *R. hilli* also tends to have a slightly more opaque and finer sculpture on head and alitrunk. Whether the two populations represent separate species remains to be decided.

[19] In the Flinders Ranges of South Australia, where I searched intensively for *Rhytidoponera*, I found only three of the larger species (*R. metallica* was also present). Of these, the largest and most tolerant of xeric conditions, and hence the most continuously widespread species, is *R. mayri*. The smallest clearly agrees with *R. convexa*, which is usually thought of as a tropical Queensland species. The middle-sized species of the three is similar to *maniac* [18], but it is a little larger and is more heavily and rugosely sculptured over head and alitrunk. With *convexa*, this middle-sized species occupies the more moderate localities within these largely very arid ranges, especially such moister localities, often with some woodland cover, as Mt. Remarkable, Wonoka Creek and Wilpena Pound. I have not been able to match this species satisfactorily with any of Clark's (1936) descriptions. The name *nigra* could possibly apply to it, but it seems more likely that *nigra* is Clark's designation for the Flinders Ranges populations of *convexa*; his description and figures are not good enough to make the identification certain. (A belated look at specimens of *R. nigra*, determined by Clark and belonging to the original series from which he described *nigra* [Owieandana, South Australia, Hale and Tindale leg.], establishes, as far as I am concerned, the synonymy of *nigra* with *convexa*. I have not changed the list to indicate this synonymy.)

[20] *R. mayri* was described from material erroneously labeled as having come from New Zealand, but which probably came instead from the hinterland of Adelaide, South Australia. Dr. Wilson has been able to compare material from various localities with the *mayri* type, and he has been able to make a very close match with specimens from Mildura, Victoria (F. H. Taylor leg.), these latter matching in turn Clark's concept of the "mallee species," *R. dixonii*. The samples of the *mayri* complex come from many arid inland localities in the southeastern quarter of Australia, ranging from southwestern Queensland through western New South Wales and Victoria into South Australia. The complex is not known from south-central Australia, and it is not yet known to extend continuously, or even as a chain of isolated populations, across the arid inland of South and Western Australia. *R. mayri* complex is absent from, or at least very uncommon in, the extreme south of Western Australia, but is met again in the dry country to the north and northeast of Perth. Specimens from Geraldton and the Mullewa area, more or less near to the coast of Western Australia, are very like eastern *R. mayri*, and show a large part of the same variation in size, head shape, color, sculpture, pilosity and especially node shape, that marks the eastern series. Going farther inland, at Meekatharra, Wiluna, Lake Violet and Yandil, W. A., (leg. W. M. Wheeler, P. J. Darlington), one encounters populations with a larger proportion of reddish individuals, and in which the rugosity of the body, especially the pronotum, tends to be reduced and looser, with wider, very finely reticulate sculpture in the interspaces. Both *occidentalis* and *glabrior* (as represented by specimens in the MCZ determined by Clark) appear to represent the more southerly, more coastal type with heavier sculpture, which I do not feel from present evidence should be nomenclatorially separated from *mayri*.

Clark relied heavily on the shape of the petiolar node in separating what he thought were different species, but it seems that he failed to realize the amount of variation in this segment. In both the eastern and western populations, and also in single nest series, one can find nodal variation completely exceeding the narrow limits Clark apparently allowed. Variation is strong in other characters, also, particularly those already mentioned.

Some series have numerous short, erect hairs over the body and appendages, others are bare or nearly so. The striolation of the gaster, particularly of the second segment, varies from transverse, through strongly arched, to longitudinal. In the population called *quadriceps* by Clark, from Tennant Creek and the MacDonnell Ranges (Mt. Frances, leg. G. F. Hill) of Central Australia, the short erect hairs are abundant everywhere on the body, limbs and scapes, and the second gastric tergite is longitudinally striolate. The sample described as *stridulator*, from inland New South Wales, is intermediate between *quadriceps* and South Australian populations in having the average second gastric segment with longitudinally arched striolation; the short hairs are mostly erect, with a sparse growth of appressed, pubescence-like hairs also, especially on the gastric dorsum. The extreme *quadriceps* variant may represent a case of character displacement in the *mayri* population of the MacDonnell Ranges, because a very similar species is known from there in *R. mirabilis*, a form notable for its virtual lack of erect hairs and for the substitution of a rather dense pubescence-like pilosity of short, appressed to decumbent, fine hairs; it is also worth noting that the dorsigastric striolation of *mirabilis* is weakly arched-transverse in contrast to the longitudinal orientation of the *quadriceps* sculpture. At present, this interpretation must be considered a very tentative one, awaiting more material from the MacDonnell Ranges and from areas between these mountains and South Australian districts in the known range of *mayri*. In my own collecting at Tennant Creek, and around Alice Springs in the heart of the MacDonnells, I found no *mayri*-group species (beginning of cold season), but took numerous samples of *taurus*, *incisa* and one or two other large species. Apparently, the *mayri* group is near the limit of its range here, in an area largely dominated by *taurus* (a large species that is similar in many ways).

R. petiolata refers to specimens from northeastern South Australia with "dome-shaped" nodes (type loc.: L. Killalpaninna, S. A.). Specimens in the MCZ from this general area (Cooper R., leg. Reuther; L. Callabonna, leg. Zietz) have rounded nodes much as indicated by Clark for *petiolata*, but nodes similar to these can also be found in series from the Flinders Ranges in South Australia (Brown leg.). The *petiolata* kind of petiolar

node seems, therefore, to be only a part of the normal variation of *mayri* in South Australia. The variation already cited for *mayri* is of the kind that would undoubtedly be described by ornithological colleagues in terms of the "polytypic" species, with the various species of Clark mostly ranking as races. It seems preferable, however, that future students of this very interesting group be encouraged to examine it from the viewpoint of independent character variation studies. Another point worth study in the future is the relationship of *mayri* to *aciculata* [9].

[21] The *metallica* complex deserves a full-scale study which, when it comes, will undoubtedly furnish wonderful data on geographical variation. The species *metallica* is one of the most abundant, easily collected and variable of Australian insects. I have examined the specimen in the British Museum labeled "type" and here designate it as lectotype; the specimen with others, is from Adelaide. These specimens are, of course, old ones, and their color may have changed, or they may have come from some distance away from Adelaide proper. However this may be, they can be matched rather closely by certain specimens taken by myself in the Adelaide district in 1950 and 1951. Here the color varies from metallic green to purple with green overtones.

As one travels northward in the dry Flinders Ranges of South Australia, the color of *metallica* series gradually and rather irregularly shifts more and more toward a uniform dark purple, and dark purple clearly predominates in the series I took around Alice Springs, in central Australia. It is to this northern desert variant that Wheeler gave the name *purpurascens*. Clark's *pulchra*, from farther west, does not seem to differ from this dark form in any significant way, at least judging from his description. *R. caeciliae* doubtless belongs here also; I have had a hurried look at a cotype in USNM.

In country with somewhat better rainfall, such as the south Victorian savannahs and the New South Wales tablelands, *metallica* workers are more often predominantly green, though with purplish tones usually present on the sides of the alitrunk. Northward in New South Wales and Queensland, one meets a form in which the alitrunk is predominantly reddish-violet,

shading into golden on the lower pleura, and with the green restricted to a mid-dorsal strip, or even absent. The gaster of most such specimens, unlike that of the central desert populations, is solid, bright green. In some places, especially at the University of Queensland Farm at Moggill, near Brisbane, I found what seemed two slight color forms living side by side under stones in sparsely-treed savannah; one of these was the form just mentioned, while the other was noticeably more completely green. The difference is still visible in the cabinet series obtained, but it was more obvious as seen in the many living colonies opened in the field. Besides color, I can find no constant differences between these series. Whether this variation marks two sibling species cannot be determined from such casual and incomplete evidence, but the possibility cannot be overlooked. These same two color forms are connected by all degrees of intermediate coloration in other localities, especially farther south, but it is possible that this is only another case of "character displacement" [14]. However, there was no obvious sign of ecological segregation between the two forms at Moggill.

In the far north of Queensland, in the Mareeba-Koah district, the open monsoonal sclerophyll woodland and savannah woodland supports an abundant population of a smallish, rather uniformly dull green *metallica*-like form, quite distinct from the more southern types. However, we do not know how these populations hook up west and south of the Atherton Tableland, so it is impossible to say whether the Mareeba district form is an independent species (*malcdicta*?) or not [31].

In addition to the extensive and striking variation in color, *metallica* shows a range of minor differences in size, shape of head and of petiole, length of appendages, sculptural details, and so on.

Crawley's var. *varians* is a form in which the superficial punctures of the gastric dorsum are coarser and more numerous than usual. But such variants are found not only in the Darling Range, Western Australia, the *varians* type source, but also in various parts of southeastern Australia. Intergrades to forms with weak or obsolescent punctures are found both east and west, so that *varians* cannot be considered as a separate population. It is interesting to note that sculptural variation shows no

geographical concordance with color variation over broad areas, at least in the fairly abundant material present in the MCZ. Part of the *varians* type material was teneral, it should be noted.

The *metallica* complex is represented in the extreme southwest by *inornata* [14], in the far north by *borealis* and *trachypyr* [11, 23], and in moister parts of the southeast, by *tasmaniensis*. All of these species are very nearly or completely non-metallescent, and in their more brownish or reddish color phases, they resemble one another, to the naked eye. *R. tasmaniensis* meets and intermingles with *metallica* at various points in the savannah country of western Victoria, in the environs of Melbourne, and on the New South Wales tablelands, but the two remain distinct and easily separable at a glance at the living colony, even when their galleries are only a few feet apart. However, teneral specimens of *metallica* isolated in the cabinet may be mistaken for *tasmaniensis*, since apart from color, the two species are closely similar. The var. *cristulata* Forel is the same as *tasmaniensis* (Emery, 1912:79); types have been compared by Wilson. *Tasmaniensis* is brown or reddish brown in color, the gaster darker brown and sometimes faintly bronzy in tone.

[22] I took a few workers of *R. reflexa* from a small nest on the Koolpinyah Track, near the western entrance of Koolpinyah Station, Darwin district, Northern Territory, Australia. Koolpinyah, one of the original localities, is here selected as type locality. My nest was taken in the middle of a typical, broad floodplain savannah, flooded by heavy soil covered with hard, lumpy earthen hillocks up to 15 or 20 cm. high and about the same in diameter, formed by an unknown agency. This savannah, shallowly flooded in the wet season (my visit was made in the early dry season), is characterized by widely scattered, spindly, low *Melaleuca* and *Banksia* trees, and by a poor ground cover consisting of sedges and certain special flowering herbs. The ants taken here, while not abundant, are special forms not seen elsewhere during my stay in the Darwin area; they include *R. reflexa*, a species of *Polyrhachis*, and a small, bright yellow *Monomorium*, the first two nesting in the hillocks, and the last in rotten sticks on the ground. It is possible that the ants escape part or all of the monsoon floods by means of the hillock nest sites, although

I have never seen this area myself when it was in flood, so cannot verify the surmise. Clark's description and figure of this species are rather crude and sketchy, but it is so aberrant a form that there can be little question of identifying it. Clark records it also from Bathurst Island, and it is probably widespread in suitable localities in the Darwin area. It will be interesting to see what happens to *R. reflexa* when and if the projected rice-culture areas are begun there.

[23] I took *R. reticulata* in open savannah woodland at Katherine, Northern Territory, on July 4-5, 1951. Workers were foraging from a single small craterless nest entrance in the hard soil. Males were present; like the lighter-colored workers, they are yellowish-brown. Foraging is nocturnal.

[24] *R. rufiventris* was originally described as a variety of *R. convexa*, but the two are quite distinct in size, shape of head and petiole and in their distribution, although they are sympatric over very large parts of Queensland. *R. rufiventris* is common and conspicuous in the open forest country of north Queensland; in Western Australia, it appears to be widespread but erratic and local in occurrence. The MCZ has specimens from this state labeled as from the Fortescue River (L. Glauert leg.), from Subiaco (Hamburg S. W. Australia Expedition, ex Forel Coll., det. Forel as *R. convexa* var. *violacea*), and from Derby (J. G. Campbell leg.); the last are probably part of the type series of Crawley's synonym *R. castanea*. Many of the specimens from the region west of Kuranda, north Queensland, are rather uniformly dark brown, instead of having the gaster red. I did not find this species in the neighborhood of Darwin or elsewhere along the Darwin-Alice Springs highway in the Northern Territory.

R. rufiventris needs to be considered carefully in relation to the very close forms *maniae* and *hilli* [18] and also *rufescens* [13]. From evidence present in publications and collections I have seen, it is not impossible that some or all of these forms are geographic variants of the same species. A dark brown form with red gaster, appearing superficially very like *rufiventris*

to the naked eye (when alive) occurs at Alice Springs, in the central Australian MacDonnell Ranges. However, this form is smaller and has the head shape of small *convexa*; it may represent an independent species.

[25] I have examined a specimen labeled "Typus" of *R. spoliata* from the Genova Museum, courtesy of Dott. Delfa Guiglia. This worker is further labeled as from "Kamerunga" in Queensland, probably wrongly, since the type locality cited with the description is Mt. Bellenden Ker, northern Queensland. Podenzana collected at both localities, but Bellenden Ker is the more likely locality for *spoliata*; I have other specimens taken in the Cairns-Kuranda area by T. Greaves, C. P. Haskins and others, nesting in epiphytic *Platyserium* in rain forest. Emery's brief description fits this specimen well enough, but does not mention the somewhat sunken eyes, surrounded by circular rugules. In his collection, Wheeler confused this species with *laticeps*, but *laticeps* has the gaster almost completely smooth and shining, and the rugules near the eyes do not pass circle-like around them; instead, those rugules anterior to the eye pass out radially from it (Wilson notes from type).

The species described and figured by Clark in 1936 as *R. spoliata*, from Mutchilba, northern Queensland (A. D. Selby leg.), according to a specimen sent by Clark to the MCZ, and evidently from this same series, is really *R. scabra* Mayr.

[26] I have a worker taken on the south shore of Lake Eyre North (G. F. Gross leg.) that agrees fairly well with Clark's description of *viridis*, except that in my worker, the posterior border of the head is feebly convex, not concave. The head is narrower behind than in *metallica*, the scapes are longer, the striation of the second gastric segment is finer, and the size is a little larger.

[27] There is a worker type of *R. tenuis* in the MCZ which, although it is headless, otherwise matches very closely three specimens from Cairns, Queensland (W. M. Wheeler leg., 1914). Cairns and Mackay (the type locality) are about 400 miles apart, so it is possible that *tenuis* ranges along most of the

northern Queensland coastal strip. This small brown species is easily recognized by its moderately elongate head (HL 1.10-1.18 mm.; CI 72-75) with transverse, slightly convex occipital border (a slightly concave median portion is seen in some views), long scapes, and large, strongly convex eyes. Spaces between foveolae of alitrunk, sides of alitrunk, node and a broad posterior strip on the postpetiole, densely and finely reticulo-punctulate and opaque.

RHYTIDOPONERA PENINSULARIS sp. nov.

Holotype worker: Very similar to *R. tenuis*, but differing in sculpture. TL 4.9, HL 1.18, HW 0.87 mm. (CI 74), WL 1.61 mm. The foveolae or coarse punctures are larger and more closely contiguous, with strongly shining bottoms, and such interspaces as exist are mostly more or less smooth and notably shining, not densely punctulate as in *tenuis*. On the sides of the posterior alitrunk, the sculpture tends to form indefinite oblique costulae that run over the top of the propodeum and become very distinct where a few of them cross the propodeal declivity, where the interspaces are very smooth and shining. As in *tenuis*, the postpetiole is finely and regularly arched-striate, but the striation continues back to the posterior tergital border (replacing the punctulate band of *tenuis* there) and surrounds concentrically a posteromedian area where the striae form a longitudinal fusiform pattern. The posterior reticulo-punctulate band of *tenuis* is not present in *peninsularis*. Second gastric segment shining, superficially arched-striate in front, becoming smooth behind, with scattered inconspicuous punctures; no fine reticulo-striate pattern as in *tenuis*.

In addition to the sculptural differences, *peninsularis* has a slightly thicker and more squarely-cut petiolar node, as seen from the side. The anterior and dorsal slopes are separated by a more abrupt angle, and the posterodorsal angle slightly overhangs the posterior face. Color medium brown.

Holotype a single worker [MCZ] from the Rocky Scrub (rain forest) in the Mellwraith Range, northeast of Coen, Cape York Peninsula, Queensland (P. J. Darlington leg., June 19, 1932).

R. tenuis and *R. peninsularis* are distinguishable from all species of similar size and color found in northern Queensland by means of their elongate head (CI distinctly less than 80, and perhaps normally under 76) and generally convex occiput. The related species *R. kurandensis* and *R. chnoopyx* have shorter heads (CI normally 80 or more). The common *R. victoriae* is distinct from all of these species in having a short, broad head with broadly concave occipital border and salient occipital angles; also, *victoriae* has very short scapes that reach or barely surpass the occipital border, in contrast to very much longer scapes for the other four species. There are, of course, other differences as well, but the features mentioned should serve to distinguish the small brown species at present known from northern Queensland. [15, 16, 31]

[28]

RHYTIDOPONERA TRACHYPYX sp. nov.

Holotype worker: With the general form of *R. metallica* and relatives, especially *R. borealis*. Size a little larger than that of *borealis*, but smaller than the average for *metallica*. TL 5.1, HL (including clypeus and occipital lobes) 1.22, HW 1.06, WL 1.66, petiole L 0.45 mm. Head narrower than in the average *metallica* worker; CI 87; occipital angles very prominent; posterior border seen in full-face view rather deeply concave. Antennal scape slender; when laid straight back from insertion, overreaching the occipital border (at the point of intersection) by a distance greater than the length of the first funicular segment. Petiolar node as in *borealis*, i.e., similar to that of *metallica*, but more rounded above.

The best characters are in the gastric sculpture. Large punctures of petiole and postpetiole coarse, deep and close together, with shining bottoms. Between these deep punctures the surface is finely and densely reticulo-punctulate and obscurely rugulose, the orientation predominantly longitudinal. The succeeding segment is longitudinally costulate, the costulae being numerous and distinct, although becoming more irregular and tending slightly to anastomose anteriorly. Intercostal spaces finely reticulate, and with scattered large punctures. By comparison, *R. borealis* has each of the two segments finely and densely reticulate-striate

in a pattern arching over median posterior areas of fine reticulopunctulation; scattered over both segments are large punctures which, however, are shallow and sculptured like the surrounding surface.

Color brownish-red, legs more yellowish; petiole and gaster piceous, appearing nearly black to the naked eye. This color is much as in *borealis* and some samples of *tasmaniensis*, although *borealis* frequently is darker over head and alitrunk. Other characters much as in *borealis*.

Holotype a single worker taken foraging in the late afternoon on the sandy river bank at Katherine, Northern Territory, Australia (W. L. Brown leg.); deposited in the Museum of Comparative Zoology.

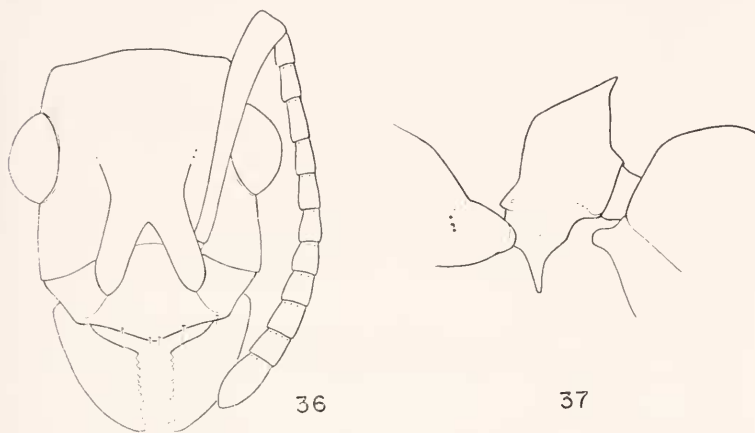
Paratype a single worker in the MCZ, labeled, "Darwin, N. T." in W. M. Wheeler's hand. I consider it likely that this is not the precise locality, but represents instead a shipping point or base locality for the collector (possibly Wesselmann). Other ants, such as *R. taurus*, in the MCZ collections bear similar labels, but it is virtually certain these were collected much farther south, near the center of the Northern Territory. The upper parts of the Northern Territory, nearest Darwin, are occupied by the closely related common species *R. borealis* [11], and present indications are that *R. trachypyx* may replace the latter in the drier savannah woodland zone of the central Territory.

[29] RHYTIDOPONERA TYLOXYS sp. nov., Brown and Douglas
(Figures 36, 37)

Holotype worker: TL, adjusting downward for expansion of gaster 7.8, HL 1.57, HW 1.19 (CI 75), L head with closed mandibles 0.93, scape L 1.32, greatest diameter of eye 0.50, WL 2.37, petiole L 0.62, gaster L, greatly extended, 3.46 mm.

Details of form of head, mandibles, antennae and petiolar node with adjacent segments as shown in Figures 36 and 37. Alitrunk convex in profile, highest in mesonotal area, with a very shallowly concave portion along the propodeal dorsum. Promesonotal suture fine but distinct; other sutures obliterated on

dorsum of alitrunk. Pronotum evenly rounded, its lower left-hand border not forming the acute tooth (this tooth is an important generic character), but instead produced only as a sub-rectangular (actually slightly obtuse) angle. The border on the right side forms a more conventional toothlike projection, but even this is not so conspicuous or acute as is usual for the genus.



Figures 36 and 37. *Rhytidoponera tyloxys* Brown and Douglas, sp. nov. Fig. 36, full-face view of head. Fig. 37, side view of petiole and adjoining structures.

Sculpture characteristic. The body, with mandibles and appendages, is very finely and densely punctulate and opaque, except that the posterior half of the gaster has the sculpture shallower and weakly shining. In addition, there are abundant coarse, shallow umbilicate punctures or small foveolae (not interrupting the punctulation), contiguous to subcontiguous on head and pronotum, becoming smaller, spaced and indistinct on mesonotum, sides of alitrunk and petiolar node; nearly or quite obsolete on propodeum and postpetiole. Between the foveolae on the clypeus and dorsal surface of the head are longitudinal rugulae that fan outward over the vertex and become lost in a reticulum behind the eyes. The punctulation of the mandibles passes into fine striation apicad.

Body largely devoid of conspicuous erect pilosity, those hairs remaining being mostly short and stiff: about 10 on anterior clypeus; a few on masticatory and ventrolateral mandibular borders; a few on oral border of gula and on smaller mouthparts; about 4 along the extensor surface of each scape, and a group at each tip of scapes; a circlelet on each funicular segment; a widely spaced pair on the pronotal dorsum; a few on the legs, including the coxae; a row across the posterior part of the postpetiolar sternum; a spaced short pair on the middle of the second gastric segment; a circlelet around the posterior borders of the second and succeeding gastric segments, the hairs becoming longer toward the apex. In addition to the erect hairs, there is a sparse growth of fine, small, inconspicuous, appressed or decumbent hairs, one each in most cephalic foveolae and in a few of the foveolae elsewhere, also forming a very dilute pubescence on scape, mandibles, gula and on legs and gaster. Color deep orange-brown, the head, alitrunk and petiole a trifle darker than the appendages and gaster.

Holotype [Western Australian Museum, Perth] one of a series of seven workers taken by Mr. K. C. Buller at Woodstock Station, about 900 miles north of Perth, Western Australia, in June, 1952. Paratypes: the remaining six workers in the type nest series differ from the holotype only very slightly in dimensions and proportions; the holotype is about average for the series. Some workers have the convex median portion of the occipital outline slightly emarginate at its summit; there is some variation in the distinctness of the inferior pronotal teeth and in the length, thickness and acuteness of the posterodorsal process or tooth of the petiolar node, some specimens having this point slightly less sharp and salient than as shown in Figure 37. There is also some difference in number and position of erect hairs, but this is at least partly due to abrasion of the integument. From the few other *Rhytidoponera* with petiolar node produced to an apical point, *R. tylosys* can be distinguished immediately by means of the structure of its head, particularly the large eyes, and by the peculiar sculpture.

[30] Wilson manuscript notes on comparison of types in the Forel Collection: "*R. haeckeli* and *R. turneri* are closely related

but distinct species. In *haeckeli*, sculpture of posterior half of head consists of fairly regular rugae which originate in the space between the frontal lobes and radiate outward toward the occipital corners. In *turneri*, sculpture in the same area consists of a solid rugo-reticulum with no orientation." *R. lamellinodis* Santschi also belongs to this group of species, which have high, angulate propodeum and thin, scale-like, dorsally emarginate petiolar node. Differences, if any, separating *haeckeli* and *lamellinodis* remain to be clarified.

[31] *R. victoriae* is a common and widespread eastern Australian species, ranging from Mt. Spurgeon, northern Queensland (P. J. Darlington leg.) around the moister eastern and southeastern fringes of the continent to the grasslands of Western District in Victoria. It is the smallest of the common Australian members of its genus, and is a familiar inhabitant of home gardens in the suburbs, and even in the large central parks of a city like Melbourne.

The variants called *modesta*, *serobiculata* and *cedarensis* were never satisfactorily distinguished from *victoriae*, and it seems that they were described only because Emery and Forel lacked sufficient material of *victoriae* to appreciate the extent of its variation. Wilson has now been able to compare the types of all these forms in the Emery, Forel and André collections, either directly or with samples furnished from MCZ. *R. modesta* is a variant showing very feeble bluish metallescence over a blackish or piceous ground pigmentation; this form is most prevalent in moist forests and upland grassy clearings in southeastern Queensland. In northern Queensland, the ground color varies from dark to very light brown in fully adult workers; and metallescence is not present. In northern Queensland also, especially near Kuranda, the gastric sculpture shows extremes of variation in the fineness and coarseness of the post-petiolar and gastrodorsal striation. It is not possible from the present material to rule out entirely the occurrence of more than one sibling species in northern Queensland, but now it seems better to take the conservative course in recognizing only the single species *victoriae* as representing the complex in northern Queensland.

R. maledicta, described as a race of *victoriae*, seems distinct in lacking a well-defined posterior scrobal area; the corresponding area is coarsely rugo-reticulate instead of longitudinally rugo-striate. The relationship of *maledicta* to the dull-green North Queensland *metallica*-like population needs study [21].

[32] The *Chalcoponera hilli* described by Clark in 1941 becomes a homonym of *R. hilli* Crawley through the merger of the two genera, a fact duly noted by Donisthorpe when he proposed the new name *clarki* to replace Clark's *hilli*. The MCZ has cotypes or nidotypes of this large, robust, *metallica*-like brown species; these specimens lack metallescence entirely. It seems likely that Forel's *obscurum*, an earlier but also preoccupied name, applied in part to the same form. Forel mentioned that some specimens had greenish heads, but it seems possible that he may have had mixed samples, including some large examples of *metallica* with faded or otherwise obscured metallescence on head and especially on alitrunk, petiole and gaster. The available name is *clarki* Donisthorpe. This species apparently is not common, and is found only along the central Queensland Coast and on certain Barrier Reef islands.

[33]

THE RHYTIDOPONERA OF NEW CALEDONIA

So far as our present information goes, there are seven species of *Rhytidoponera* on New Caledonia and the islands on its coasts. This figure includes two species described here as new, and leaves out two now placed as synonyms. Undoubtedly there yet remain species to be described, particularly from the poorly-known highlands of the north and from the coastal islands, but a key should help to make further study easier.

Up to now, most of the work on the *Rhytidoponera* has been done by Emery (1883, 1914), although André and Viehmeyer each described a single species. Unfortunately, in his 1914 paper, Emery momentarily confused the two common species *R. fulgens* and *R. numeensis*, so that most of his remarks on *numeensis*, at least on the workers, actually apply to *fulgens*. In this work he described the real *numeensis* over again as *acupuncta*. The suspicion that some such mixup applied here has been fully confirmed, and the confusion itself finally cleared, by Wilson's

examination of the types and other specimens in the collections of Emery (Genoa) and André (Paris), with fresh specimens of the species concerned at hand for comparison. Wilson has also noted that the type of var. *soerula* differs from "typical" *fulgens* chiefly in the more definitely oriented rugation of the head (longitudinal) and alitrunk (transverse, especially on pronotum); in Wilson's extensive series from the southern half of New Caledonia, one can find all degrees of intergradation linking extremes of the two kinds of sculpture, without particular territorial attachment of the variation.

Along with the two new species he collected in the country, Wilson's most helpful contribution is the detailed information contained in his notes on the distribution, ecology and behavior of the New Caledonia species. This information can be summarized as follows. Collections were made in several localities, both disturbed and relatively undisturbed, in the southern half of New Caledonia. In all of these localities, at altitudes below about 800 m., there occurred the large metallic green species, *R. fulgens*, and usually also the smaller, black or brown species, *R. numeensis* and *R. pulchella*. At three of the forested upland localities, there was found a new small species close to *numeensis*, but with a thinner node. All of these species were taken foraging during broad daylight on low foliage in the forest understory or at the forest border, and all of them were taken in Berlese funnel samples from the forest floor leaf litter. Mostly, their nests were found under rocks in the soil, but occasionally one or more of these forms nests in rotting wood.

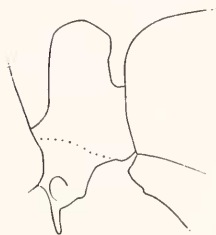
A second new species of the small-sized group was taken twice at a single locality (*R. versicolor*, Montagne des Sources), at altitudes of about 800 and 1000 m.; significantly, no other members of the genus were seen at these altitudes at this locality, nor, except for *R. acanthoponeroides*, were any other species of *Rhytidoponera* taken above 800 m. anywhere by Wilson.

The food of these species, so far as observed, consisted of small arthropods, some of which were certainly taken alive. To what extent the New Caledonia *Rhytidoponera* feed on plant sugars and other foods is not yet known.

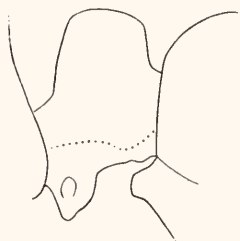
The brief review of the species offered below is based on Wilson's ample collections from New Caledonia, made during December, 1954, and January, 1955; smaller samples, all from the vicinity of Noumea, were sent me by N. L. H. Krauss.

Key to the Rhytidoponera species of New Caledonia — workers

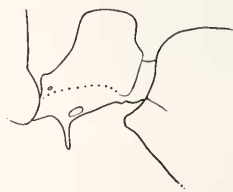
1. Larger forms, full length of alitrunk (WL) exceeding 2.0 mm.; body color of mature specimens with rich metallic green or purple tones . . . 2.
 Smaller forms, full length of alitrunk (WL) less than 2.0 mm.; body color black, brown or combinations of these with red or yellowish; no metallic colors 4.
2. Petiole produced backwards as an acute apical tooth; gastric dorsum smooth, with only shallow traces of coarse punctures, the surface cloudy with a bluish opalescence *acanthoponeroides* Vieh.
 Petiole bluntly subtruncate or rounded above, not produced as a tooth from the apex; gastric dorsum largely or wholly striate or reticulate . . 3.



38



39



40

Figures 38-40. *Rhytidoponera* spp. from southern New Caledonia. Workers, side view of petiole and adjoining structures. Fig. 38, *R. wilsoni* sp. nov., paratype. Fig. 39, *R. numeensis* André. Fig. 40, *R. versicolor* sp. nov., paratype.

3. Coarse sculpture of body overlain by finer sculpture, rendering the surface largely opaque; postpetiole and succeeding segment very finely reticulate *atropurpurea* Emery
 Coarse punctures of body shining, without overlying fine sculpture of much account; postpetiole and succeeding segment transversely- to arched-striate *fulgens* Emery

4. Ventral process of petiole forming a long, straight, very slender spine; the small oval fenestra is situated behind the spine near its base (Fig. 40) 5.
 Ventral process of petiole not wholly slender spiniform, but more subtriangular, irregularly tapered, and much broader, wholly containing the oval fenestra (Figs. 38, 39) 6.
5. Gastric dorsum, especially of the second segment, covered densely with fine whitish pubescence which nearly obscures the finely reticulate-striolate sculpture of much of its surface; color black, with brown legs, mandibles and antennae, becoming yellowish toward the apices ...
pulchella Emery
 Gastric dorsum very smooth and shining, except for some feeble striation across the postpetiole anteriorly; pubescence very sparse and inconspicuous; color mahogany or piceous, the gaster orange, brown or piceous; legs, antennae and mandibles yellow throughout (Fig. 40)
versicolor sp. nov.
6. Petiolar node strongly compressed anteroventrally, its ventral process narrowed to a digitiform apical portion; spaces between pronotal punctures not densely and finely striate (Fig. 38) *wilsoni* sp. nov.
 Petiolar node not strongly compressed anteroventrally, its ventral process without a digitiform apical portion; spaces between pronotal punctures densely and finely striate (Fig. 39) *numcensis* E. André

RHYTIDOPONERA ACANTHOPONEROIDES Viehmeyer

This species was described from a single worker from New Caledonia, locality unspecified. It has not been reported since the description, but now Wilson has taken a colony on Mt. Mou, north of Païta, under a stone in an opening in cloud forest dominated by *Araucaria* and *Podocarpus* on the summit ridge below the summit, altitude probably somewhere near 1000 m. This sample fits the original description well except for the color, stated to be "dark brown, with more yellowish brown appendages and mandibles; body steely blue." Viehmeyer describes the smooth gastric dorsum well, with its cloudy blue-gray opalescence; Wilson notes that his samples were predominantly metallic green while alive, and these were the colors seen in the specimens as they came out of alcohol two months after capture. After two years in the dry state, they have changed to a predominantly bluish-purple over head and alitrunk; the legs are a contrasting

light reddish, as are also the mandibles and antennae. The worker of this species is unmistakable because of the postero-dorsally mucronate petiolar node, found in no other New Caledonian species, but occurring in similar form in several Australian *Rhytidoponera*, as well as in other ectatommine genera in both hemispheres.

The male (previously undescribed) measures TL 7.1, HW 1.30 (across and including compound eyes), WL 2.41, scape L (excluding basal neck) 0.27 mm. Scape only about twice as long as broad, twice as long as the first flagellar segment, and half as long as the second flagellar segment. Mesothorax robust; notauli distinct, impressed, forming a complete "Y." Wing venation of the complete type; fine traces are present of first radial crossvein in one of two male specimens examined. Hindwing (of measured specimen and one additional specimen) with 6-8 subapical and 0-3 submedian hamuli.

Petiole nearly twice as long as high, feebly arched, profile rising slowly from front to gently rounded summit near posterior end; ventral process lacking (ventral process of worker is of the *versicolor* and *pulchella* type, Fig. 40). Genital capsule a little more elongate than in some other species of the genus; parameres and hypopygium (IX sternite) rather more slender than average, the latter rounded apically. Penis valves obliquely truncate at apex, the corners rounded off.

Integument predominantly smooth, moderately to strongly shining, on the body overlain by weak bluish opalescence; certain areas slightly roughened or vaguely punctulate, such as the dorsum of head mesad of compound eyes. Propodeum and petiole more definitely roughened, the latter opaque, and with a few superimposed, separated rugae.

Pilosity of abundant fine light brown hairs, more tapered and mostly more curved than in the *numecnsis* male. Pubescence dense, appressed to decumbent, yellowish-gray and conspicuous over most of body and appendages. General body color dark brown (with faint opalescence), head darkest; mandibles, legs, and antennae lighter; genital capsule yellowish.

RHYTIDOPONERA PULCHELLA Emery

Emery (1914) noted the variation in size and gastric sculpture shown by this species, evident in the extensive series before me. The largest of these are as large as large *numeensis*, while the smallest are slightly smaller than the smallest *versicolor*, so that *pulchella* just about matches the total size variation of the other three small New Caledonian species taken together.

This species is readily distinguished by the shape of its ventral petiolar process, which is like that of *versicolor* (Fig. 40), by the conspicuous whitish pubescence of the second gastric segment, by the fine, centrally obsolescent sculpture of this same segment, which is consequently rather strongly shining under its vestiture, and by the more or less yellowish apices of the antennae and tarsi, and edges of the mandibles, which contrast with the black of the body. Both Wilson and Krauss found this form rather common in relatively moist forested localities all over southern New Caledonia. It nests commonly under stones in the earth.

RHYTIDOPONERA NUMEENSIS E. André

An average worker of this species measures 5.5 mm. TL; the HL is 1.28, HW 1.15, WL 1.82 mm.; CI 90, ex Mt. Mou, No. 147. This dark brown species is the commonest and ecologically most tolerant of the smaller *Rhytidoponera* of the island. It is easily recognized by its light reddish legs and antennae, contrasting with the darker body, by the robust build, by the striation mixed with the coarse punctures of the alitrunk, and by the shape of the ventral process of the petiolar node (Fig. 39).

Wilson found *numeensis* foraging on the ground and on foliage, together with *pulchella*, and, in forested areas in the hills, with *wilsoni*. It was not taken in southern New Caledonia above 800 m., and the majority of collections came from below 500 m. This species nests in rotten wood where it is available; Wilson's nests were taken in rotten branches lying on the forest floor, as well as in larger, moss-covered logs. In shaded pastures and other disturbed areas, more nests of this species seem to occur under rocks in the ground. Colonies were usually small, with 100 workers or so, but one or two larger nests were seen. In one nest, the larvae were seen feeding upon a small talitrid amphipod.

RHYTIDOPONERA ATROPURPUREA Emery

I have not seen this species, and Wilson's notes do not mention the type material. Emery's description compares it with "*Rh. numecensis*" chiefly; as mentioned already, he was really referring to *fulgens*, but curiously enough he also mentions *fulgens* by name in the description. At any rate, the picture emerges of a large form similar to *fulgens*, but with a superficial, finely reticulate sculpture overlying the coarser sculpture, and replacing the striation of the gastric dorsum so characteristic of *fulgens*. The color is cited as "violaceous black; mandibles, funiculi, legs and apex of gaster deep brown." The male is stated to be like that of *fulgens*, except that the gaster is subopaque, finely and superficially reticulate. Known only from Ouedjo I., near Hienghiène, in the northern part of the main island.

RHYTIDOPONERA VERSICOLOR sp. nov.

(Figure 40)

Holotype worker: TL 4.5, HL 1.04, HW (excluding eyes) 0.92 (CI 89), WL 1.38, scape L 0.90, max. diameter eye 0.22 mm. Similar to *numecensis*, but smaller and less robust. Occipital border of head feebly and broadly concave in full-face view, but occipital angles gently rounded; as seen from the side, the posteroventral corners a bit better developed and more nearly rectangular. Clypeal apron distinct, translucent, forming a bluntly rounded angle in the middle. Alitrunk lower and more slender, in profile forming a single convexity, with only the propodeal declivity breaking the outline slightly as it falls off steeply from the dorsum. Petiolar node (Fig. 40) much lower than in *numecensis* (Fig. 39), and with the ventral process very long and slender, like that of *pulchella*. Seen from above, the node is only slightly broader than long (much broader than long in *numecensis*).

Head, alitrunk and petiole coarsely reticulopunctate throughout; a few of the dorsomedian rugules on the head forming longitudinal costulae (including a median carinula), but the sculpture otherwise without definite orientation, and without the interspersed striation so widespread in *numecensis*. Gaster smooth and shining, with scattered small piligerous punctures;

postpetiole with a few indistinct striae arching from the sides across the anterior face. Erect pilosity much as in *numeensis*, the hairs fine, whitish, abundant on all parts, uneven in length. Appressed pubescence extremely sparse except on extremities of antennae and legs.

Head, alitrunk and petiole deep mahogany (nearly black to naked eye). Gaster bright orange-yellow. Legs, antennae and mandibles clear yellow.

Holotype [MCZ] from near the Dumbéa Road, just below Montagne des Sources, New Caledonia. This locality is mixed forest, mainly angiosperm evergreens, but with large *Araucaria* and *Agathis* prominent in the upper story, surrounding the headwaters of the Dumbéa River; altitude ca. 800 m. (E. O. Wilson leg., XII-17-1954, No. 185). The holotype and several paratype workers were collected from the vegetation at the forest border during daylight hours. Another collection from Montagne des Sources (Wilson, No. 169) was made on the same day higher up (ca. 1000 m.) in second-growth *Araucaria* forest, where the workers were taken foraging on a small angiosperm shrub in the understory during midafternoon.

Variation: The workers from the upper site (No. 169) are much darker in color; the head and alitrunk are dead black or very nearly so, while the petiole and gaster are dark brown above (blackish to naked eye), medium brown below. This darker coloration is approached by certain specimens from the lower site (No. 185) with brownish-orange or brown gaster. All specimens maintain the clear yellow mandibles, antennae and legs. In several specimens, particularly in the upper-site series, the petiolar node is a little more rounded above, and the sculpture of its anterior face varies more or less toward a smooth, shining surface crossed by weak transverse rugae or costulae, becoming concentric or longitudinal on the summit. These same specimens often tend to have the obsolescent striation of the postpetiole a little better developed and extending back over as much as $\frac{2}{3}$ of the surface, which is consequently often not so strongly shining as in the holotype. A few individuals have the declivity of the propodeum meeting the dorsum through a distinct but obtuse angle, and in these, the declivity may be weakly concave as seen in side view. One specimen has a feeble impression or step in

the region of the metanotum. Variation in size and in the chief proportions is very slight; the darker specimens from the upper site average a trifle smaller. The paratypes are to be deposited in MCZ, USNM, and one or more Australian and New Caledonian collections.

RHYTIDOPONERA WILSONI sp. nov.

(Figure 38)

Holotype worker: TL 5.2, HL 1.25, HW (excluding eyes) 1.06 (CI 87) WL 1.73, scape L 1.12, max. diameter eye 0.26 mm. Very similar to *numeensis*, from which it differs principally in having a notably more strongly anteroposteriorly compressed node, with a different ventral petiolar process (Fig. 38); the posterior face of the node is concave as seen from the side. The head of *wilsoni* has a more broadly concave occipital margin (straighter in some views) and slightly more sharply rounded occipital corners than in *numeensis*. The sculpture differs in several details; generally speaking, the punctures are coarser and more closely contiguous over head, alitrunk and gaster, and the ridges between tend to form coarse, rather indefinite rugules (longitudinal on head, diagonal on sides of alitrunk, transverse on propodeum and anterior face of petiolar node) in place of the fine, dense striation of these same areas in *numeensis*. Postpetiole rather finely arched-striate, passing into a posteromedian area of finer, concentric striae that are interrupted by and interspersed with fine, indistinct punctulation. Coarse piligerous punctures of this segment very shallow, indistinct, and not so clearly elongate as the corresponding ones in *numeensis*. Second gastric segment very finely and densely striate, the pattern arched over a posteromedian weakly shining area of very superficial elliptical-concentric striation (longitudinal axis) that is very finely interrupted or coriaceous (clearcut, uniform, and predominantly longitudinal striation in *numeensis*). Coarse piligerous punctures of this segment small and inconspicuous, much smaller than the corresponding ones of *numeensis*.

Erect pilosity and appressed pubescence fairly abundant but not dense, uneven in length, the pubescence conspicuous at all only on the gaster and appendages. Color piecous, the head,

petiole and gaster lighter and a bit more reddish than the alitrunk. To the naked eye, the body appears very dark, nearly or quite black. Legs, mandibles and antennae orange-brown. Coloration in general much like that of *numecensis*.

Holotype [MCZ] a stray diurnal forager taken on foliage at 180-400 m. on Mt. Mou, north of Païta, New Caledonia (E. O. Wilson leg., XII-10-1954, No. 110). Paratype workers were taken with the holotype and at Le Chapeau Gendarme, east of Yahoué, and at Ciu, near Mt. Canala (Wilson Nos. 73, 74, 80, 84, 96 and without numbers). These were taken foraging during the daylight hours on foliage and over rocks on the forest floor. One nest was found beneath a stone; other workers came from leaf litter berlesates. The Ciu sample was very dark, and had the legs dark brown. The occipital border varied in degree of concavity. Paratypes in MCZ, USNM and elsewhere.

[34] Among *Ectatomma* species, the closest to *aztecum* (judging from the holotype, kindly sent by Dott. Delfa Guiglia) is *ruidum*. The color is dark, as in *ruidum*, but the node of *aztecum* is slightly thicker as seen from the side. The sculpture of gastric segment I (postpetiole) is slightly different in *aztecum*; the costulae are arched transversely across the anterior descending face of the segment, but otherwise are longitudinal, close and at most feebly undulant in a few places. The outstanding distinction, however, is the extreme development of the erect pilosity; this is rather short, but present in great abundance on most body and appendage surfaces. The species has never been taken a second time; its type locality is "Michoacan." Since this form is very close to the highly variable *ruidum*, it would be desirable to have additional material from southwestern Mexico in order to see exactly what the relationship is between these two species.

[35] The type locality of *E. confine* apparently lies somewhere in the present Colombia or Panama. Mayr's description is very sketchy, and the only specimen I have seen that fits it fairly well is a unique worker (Fig. 2) from Tela, Honduras (D. M. Bates leg.). This worker was found mixed with *ruidum* and *morgani* in the Wheeler Collection, and at first glance it appears to be intermediate between these two species. However, it differs from

both in the disproportionately strong development of the median pronotal eminence; this is high, somewhat compressed laterally, and forms a blunt angle as seen from the side. The lateral pronotal eminences are rather small, but their size is probably somewhat variable in this as in other species. The greatest eye diameter and the apical antennal segment are very nearly precisely the same in length, and the petiolar node is thicker than that of *ruidum* as seen from the side. The sculpture of the second gastric segment is composed of fine, sericeous striolation, as in *ruidum*.

Whether this identification is correct can only be determined after the review of more material in comparison with the type in the Mayr Collection in the Vienna Museum. It is not impossible that *confine* will finally prove to be a geographical variant of the species represented in the Amazon Basin by *morgani* [38].

[36] *E. edentatum* has been confused with *muticum* several times (Forel, 1912b:31), but the two are easily separated by eye size (see key) and sculpture of gastric segment II. In *edentatum*, the tergum of the second segment is very regularly and very finely striolate in a pattern of varying direction, and in general is sericeous-opaque. In *muticum*, the same segment has a much more indefinite and looser transverse striation that is virtually effaced over a large area distad; the surface in general is definitely shining, even glassy in the center and between striae.

Forel's arrangement of 1912 depends on characters, such as antennal proportions and metallic luster of integument, that seem too variable (and often allometric in expression) to have more than local or individual significance; neither Forel nor Santschi seems to have expended much effort in trying to define limits of variation for these forms. *E. macdonaghi* is poorly described as a race of *edentatum*, of which species it may be an ergatoid or pathological intercaste. *E. morgani* [38] may be a northern variant of *edentatum*.

[37] The names *strigosum*, *permagnum*, *confusa* and *aerea* seem to me to represent slight local variants of one species, widespread in southern Brazil and Bolivia. The name *strigosum* unfortunately must fall as a primary homonym of *Rhytidoponera strigosa* (Emery), originally described in *Ectatomma*, and Forel's

name *permagna* (emended to the proper form *permagnum*), being next available, is raised from varietal to species rank to take its place. Since *permagnum* and *lugens* are separated only by minor and variable characters and are allopatric as at present known, it is possible that these two names represent extreme geographical populations of the same species. Collections from the region just south of the Amazon are needed to decide whether intergradation is completed in this area. In addition to the sculptural differences (see key, couplet 1), which may only reflect character displacement against the closely related species *opaciventre* in the south, the samples of *lugens* I have seen have narrower heads and are generally more slender overall than are the *permagnum* examined from Bolivia and southeastern Brazil.

[38] *E. morgani* is uncommon in collections, and has remained enigmatic due to its almost universal confusion with the similar *ruidum*. MCZ has stray workers taken near Port-of-Spain, Trinidad (R. Thaxter leg., beating foliage) and in British Guiana: source of R. Essequibo (Ogilvie leg.); Kartabo vic. (W. M. Wheeler, H. O. Lang leg.). Constant characters distinguishing this species from *ruidum* (see key) are the proportionately longer and narrower head, somewhat more convex behind as seen in full-face view; eyes smaller and placed a little farther from the posterior border; scapes and legs a trifle longer; petiole thicker from front to rear, and not biconcave in side view, as in *ruidum*; fine striolation of second gastric segment less distinct basad, where it merges with some fine, dense, irregular reticulo-punctulation or broken striation (but this last character is very variable).

There is no doubt that *morgani* is really very closely related to *edentatum*, and the two forms may well be geographical segments of the same species. A worker sent by Father Borgmeier from the Mato Grosso is intermediate in some respects between my Guiana-Trinidad *morgani* samples and the few specimens of *edentatum* available from the State of São Paulo (W. W. Kempf leg.). The material available to me is not sufficient as a basis for formal action on this probable synonymy at the present time.

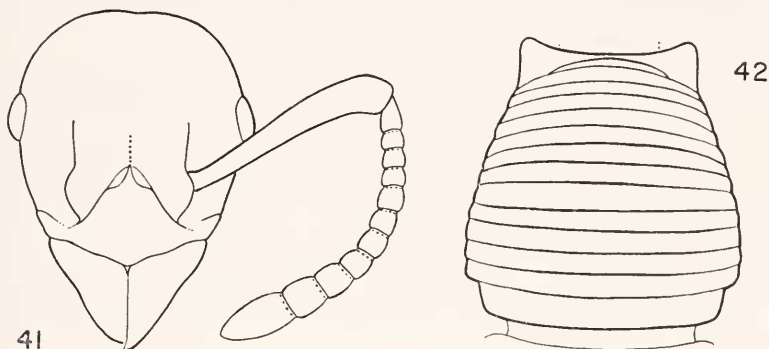
[39] *E. opaciventre* is a large species of the La Plata-Paraná drainage. It apparently does best in districts that are arid, or at least that have prolonged annual dry spells. The color is very variable, ranging from reddish through a series of bicolored forms to piceous; the variety *concolor* is a part of this variation. Shape of head and complete lack of transverse rugules on the postpetiolar dorsum distinguish this species from *permagnum*.

[40] *E. planidens* is a puzzling species very close to *quadridens* (see key, couplet 4), but both of these are present at some localities in Brazil, without known intergradation (Agudos, S. Paulo State, leg. W. W. Kempf). A small, light female from central Brazil owned by Father Borgmeier, however, appears transitional to *quadridens*, and it is not beyond possibility that *planidens* is merely a morph of the more familiar species. Wilson (MS notes) has located the probable type of *E. quadridens* in the Museum d'Histoire Naturelle in Paris; it is a specimen from the Bose Collection, now in the general collection.

[41] *E. muticum* has been confused with *E. edentatum*; the characters are discussed under the latter species [36]. The records and specimens of *muticum* I have seen indicate that this species is restricted to the dry eastern bulge of Brazil, in Ceará and neighboring states. There is only one exception to this pattern, and this exception is so far off that it is difficult to credit it. I refer to a single worker in the MCZ bearing the label "Acapulco, Mex./Fredk. Knab." and which is identical, so far as I can tell, to specimens from northeastern Brazil collected by W. M. Mann, now in the same museum. Acapulco is close to Michoacan, the type locality of *aztecum*, but this circumstance is probably only a coincidence. Until such time as the Mexican record for *muticum* is confirmed by further collections, the occurrence of the species in that country should be regarded as doubtful.

[42] *E. tuberculatum* varies widely in color and sculpture, as pointed out by Weber (1946). The greatest variation seems to focus in northern South America and the Amazon Basin, where hardly two nest series can be found that are alike. Especially

striking is the brown variant, contrasting with the more familiar yellowish types from farther north and south, as well as from this same area in the middle of the range. *E. acrista* differs modestly from *tuberculatum* in having the occipital margin of the head more rounded as seen in full-face view; I have specimens of this kind from the Paraná River, Paraguay (Fiebrig leg.). Other samples from central South America may represent transitions to *acrista* from *tuberculatum*, but at present the evidence is not as complete as it should be to dismiss *acrista* as a southern peripheral variant of *tuberculatum*.



Figures 41 and 42. *Gnampptogenys* spp., workers. Fig. 41, *G. grammodes* sp. nov., paratype, full-face view of head. Fig. 42, *G. mecotyle* sp. nov., paratype, dorsal view of petiolar node.

[43] *G. acuminata* samples in the MCZ: Campinas, Goias, Brazil (Schatzmaier leg.); Santa Helena, Bolivia (W. M. Mann leg.); Bartica District, British Guiana (A. E. Emerson leg.). Varies from ferruginous to black in color; very similar to *G. sulcata*, but differing in the more striking posterodorsal production of the node.

[44] *G. annulata*. Samples in the MCZ indicate a very wide range for this species in the Amazon-Orinoco drainage, west as far as Ecuador, Peru and Bolivia, and north to Costa Rica and Honduras. I have seen specimens from Rio de Janeiro State, and the species is reported from Santa Caterina.

The male is a little shorter than workers from the same nest, piceous with brown legs and antennae, smooth and shining except for rugose propodeum; petiole finely rugulose, shining; front of head finely punctulate, shining. Notauli complete, well-marked. Forewing with "complete" venation, i.e., Rsf2 and 3 and Mf2 and all present.

[45] Samples of *G. aculeaticoxae* were examined from Kama-kusa, British Guiana (H. O. Lang leg.), Barro Colorado Island, Panama Canal Zone (J. Zetek leg.), and from Bolivia: lower Rio Madidi and Blancaflor and Huachi on the Rio Beni (W. M. Mann leg.).

[46] In a recent paper (Brown 1957), several forms were dealt with under *Holcaponera*. Var. *antillana* Santschi was placed as a synonym of *striatula* Mayr [79], and the nominal species or subspecies *satzgeri* Forel, *spurium* Forel and *foreli* Santschi were synonymized under *simplex* Emery. The new species *mina* and *acuta* were described, and *Rhopalopone relict*a Mann was transferred to *Holcaponera*. There are some new records of *acuta* from Peru: Tingo Maria, Monson Valley; and Colonia Perene, 18 miles northeast of La Merced, Junin (E. S. Ross and E. I. Schlinger leg.).

[47] In a review of the *Stictoponera coxalis* group (Brown, 1954c) all of the species here indicated were discussed, and synonymy proposed for some of them. *S. biroi* Emery (Fig. 17) has been taken by E. O. Wilson at Bisianumu, near Sogeri, Papua, at about 500 m. A single dealate female (No. 654) and a small colony with callow winged males and females (No. 675) were taken in moist rotting logs in rain forest.

[48] *G. panda* is very close to *G. taivanensis*, but the adult color is reddish-brown (blackish in *taivanensis*), and the postpetiole of *panda* is much more closely, finely and opaquely sculptured, with the interfoveolar spaces forming distinct oblique costulae, so that the surface appears in some lights to be punctate-striate. In *panda*, the sculpture of the second segment is nearly closed in across the middle, whereas in *taivanensis* nearly the whole

dorsal-discal area is smooth and shining, with only the coarse piligerous punctures. I have seen additional specimens of *panda* from Muping (2000 m.), on the Ya An to Mou Kung track, Sikang Province, about 90-100 miles west of Chengtu, western China (D. C. Graham leg.); this locality is not far airline from the type locality near Kuanhsien, Szechuan. The petiole of *panda* is shown in side view in Figure 18.

[49] I have examined specimens of *G. bispinosa* taken by G. C. Wheeler at Changuinola district, Bocas del Toro, Panama, and by W. M. Mann in Costa Rica at Zent, Colombiana Farm and Hamburg Farm, Santa Clara Province. The Hamburg Farm series includes a male: TL 8.2, HL without cervical rim of occiput 1.28, L head with closed mandibles 1.73, HW with compound eyes 1.33, greatest diameter of compound eye 0.52, WL 2.61, petiole L 0.80 mm. Antenna: scape L 0.35, L funicular segment I 0.19, fun. II 0.55, fun. III 0.54 mm. L forewing ca. 5.5 mm. Mandibles triangular, distinctly dentate. Ocelli large and clear, set close together on a darkened callus; distance between anterior and posterolaterals less than an ocellar diameter, distance between posterolaterals slightly greater than an ocellar diameter. Notauli and parapsidal furrows very distinct, complete. Maxillary palpi with 5, labials with 3 segments. Petiolar node long and low, nearly twice as long as high, with a subrectangular ventral process in front below. Wings as in other larger *Gnamp-togenys*, Mf2 short or completely contracted, Rsf2+3 present. Body and appendages shining, completely smooth except for mandibles and clypeus, which are feebly and obscurely longitudinally striate, and propodeum, which bears a bold pattern of sharp rugae. Color ferruginous yellow; gaster yellowish-tan.

The worker of this species has a palpal formula of 3, 2.

The Wheelers have described and figured the larvae (1952a, pp. 132-133, pl. 5, figs. 1-5).

[50] *G. alfaroi*. I have examined a short series (USNM, MCZ) from Turrialba, Costa Rica (O. L. Cartwright leg.) of this very rare, local and interesting species. It is a rather aberrant member of the *mordax* group, large in size, black in color, long-headed, with short, thick mandibles. In many respects, it resembles

species of the genus *Cylindromyrmex* (Subfamily Cerapachyinae?), and the relationships between *Cylindromyrmex* and *Gnamptogenys* are worth investigation on this account.

[51] I was able to compare the female type of *G. haenschi* with workers from the lower Rio Madidi, Bolivia (W. M. Mann leg.); the workers are very similar in their robust build and very fine costulation, but they are decidedly smaller than the female. Like the type, their color is brownish red. In the worker, the petiolar node is compressed anteroposteriorly, but is not quite twice as broad as long. A female from Tingo Maria, Peru (E. S. Ross and E. I. Schlinger leg.) is similar to the type, but is much darker, nearly black in color.

[52] *G. hartmani* remains known only from the unique type worker, from Huntsville, Texas, far outside the known range of other species of *Gnamptogenys*. Creighton (1950, p. 36) gave it as his opinion that the tarsal claws of *hartmani* were simple, a condition he "regularly encountered in . . . subgenus *Gnamptogenys*." However, careful examination of the *hartmani* holotype, as well as all available species of *Gnamptogenys* and *Parectatomma* in the old sense, reveals that all have an extra tooth on each of the six pairs of tarsal claws. Among these groups, simple tarsal claws must be exceptional, if they occur at all.

[53] The dealate female type of *epinotalis* has been examined and compared with workers of the same species (Fig. 20) taken by Wilson at Ebabaang, ca. 1400 m. altitude, on the Mongi Watershed, Huon Peninsula, New Guinea, in irregular galleries in the earth under a stone. The Ebabaang locality is in mountain rain forest. The ants resembled *Ponera* in life. *G. epinotalis* is very close to *G. luzonensis* Wheeler, differing mainly in details of sculpture. The extra teeth on the posterior tarsal claws of *epinotalis* and *luzonensis* are very minute and reclinate, and are situated close to the base of each claw. They can be seen only at magnifications over 120 \times , and then only under the most favorable conditions. Dr. Chapman has turned over to me some workers of *luzonensis* taken by D. Empeso in the vicinity of

Dumaguete, Negros Oriental, Philippine Islands. These two species are among the smallest *Gnamptogenys*; and the eyes are much reduced in the workers.

Among the other small species of the Indo-Melanesian area, formerly placed in *Rhopalopone*, I have seen types of *malaensis* (Mann) and reliable specimens of *dammermani* (Wheeler) determined by Wheeler himself from Buitenzorg, now Bogor, Java (Dammerman leg.), as well as a series from the Cuernos Mts., near Dumaguete, Negros Oriental, Philippines, at about 1800 feet altitude (J. W. Chapman leg.). Wilson has compared these with the types of *cribrata* (Emery) and *diehli* (Forel), as well as with the very different *major* (Emery), on deposit at Genoa and Geneva. Wilson took *cribrata* twice at the lower Busu River, near Lae, New Guinea, in lowland rain forest leaf litter. The worker does have vestiges of compound eyes, but these are minute.

[54] Dr. Wilson has compared worker specimens from the MCZ Collection, taken at Kartabo, British Guiana (A. E. Emerson leg.), with the female type of *exarata*, and he feels that they are conspecific. He notes that the type female has a head length of about 0.93 mm., or less than females associated with the Kartabo workers, but a little larger than these workers themselves. A Kartabo female has HL 1.12 mm., compound eye L 0.27 mm. The compound eye L of the type female was about 0.23 mm. Wilson's measurements were, however, not made under ideal conditions.

The type has about 30 costulae between the compound eyes, with a possible error of about ± 1 . In the females of the Kartabo series, the costulation of the petiolar dorsum varies from concentric to longitudinal; in the type, it is longitudinal. *G. exarata* is a member of the *mordax* group, related to both *continua* and *interrupta*, but it does not compare with the types of these two species [55, 56]. In *exarata*, the anterior clypeal border is concave in the middle.

[55] The worker type of *G. interrupta* borrowed from the Vienna Museum has HL 1.12, HW 0.95 mm. The eyes are very small,

with about 12 pigmented facets, surrounded by a ring of unpigmented facets, colored like the surrounding integument. The pigmented part of the eye is slightly smaller than the greatest scape thickness, but if the unpigmented part is included, the eye diameter would more or less equal the scape thickness. The sculpture is fine, 50 ± 3 costulae between the compound eyes. Second gastric segment smooth and shining, with a few coarse punctures. Color rich ferruginous red; legs and antennae more yellowish. "Patr.? M. Dresd./Sudamerika." Like *continua*, but larger and with finer sculpture. (Lectotype.)

Specimens from Lombardia, Honduras (W. M. Mann leg.) agree well with the type, but have coarser costulation. The size variation in this series is marked.

[56] *G. continua* is the smallest known species of the *mordax* group; lectotype IIL 0.74, HW 0.58 mm.; about 35 costulae between the compound eyes; eyes themselves small, only about 5-6 facets, their diameter less than the greatest scape thickness. Sides of head subparallel; greatest width at about the anterior third. Clypeus as in *mordax*. Metanotal groove shallow, but distinct. Propodeal angles blunt, sublunate, feebly overhanging the concave borders of the declivity. Petiole approximately as broad as long, broadest behind, longitudinally costulate; anterior face of node distinct, its sculpture effaced. Second gastric segment rather finely longitudinally costulate above, but smooth and shining on the sides behind.

I have seen samples referred to *continua* from the following localities: Las Hamacas, near Santiago Tuxtla, Veracruz, Mexico (E. O. Wilson leg.); nest in a piece of rotten wood in leaf litter, tropical evergreen forest. Boquete, Chiriqui Mts., Panama (F. M. Gaige). Barro Colorado Island in the Panama Canal Zone, April, (A. E. Emerson, No. 110). Mandeville, Jamaica (A. Wight). Tingo Maria, Monson Valley, Peru (E. S. Ross and E. I. Schlinger leg.). Variation among samples extends to density of costulation, size, extent of shining area on second gastric segment, and depth of pigmentation; some series are deep reddish, others are almost black. The Las Hamacas series was most like the lectotype ("Brasilien") among my samples, even though it was on the opposite extreme of the range.

The Barro Colorado series includes a male, which is a little shorter than the accompanying workers, is dark piceous in color with yellowish antennae, legs and genitalia, and which has deep and complete notauli. The integument is smooth and shining except for the cephalic dorsum, propodeum and petiole, which are finely and densely punctulate and more or less opaque. The second and third abscissae of Rs are lacking.

Some of the Panamanian specimens have additional suturation on the alitruncal dorsum and otherwise betray themselves as ergatoid females or other worker-female intermediates. Sant-schi's Panama variety appears to be about the same as the Barro Colorado sample from the brief characterization; there seems no need to maintain his name *panamensis*. The Jamaican record of *continua* indicates an introduction, very probably made within historical times. This island has received many introduced ants from South and Central America.

[57] The three varieties of *concinna* were described chiefly on sculptural differences now recognized as individual variations that can be expected even in single nest series. This is confirmed for the type of *semicircularis*, matched with a worker from one variable nest series in the MCZ. The var. *romani* had as an additional character the color of the gaster, "entirely black." Whether this blackness is caused by decomposed gastric contents or some secondary influence, I do not know, but it does not seem likely that it is a character of specific value.

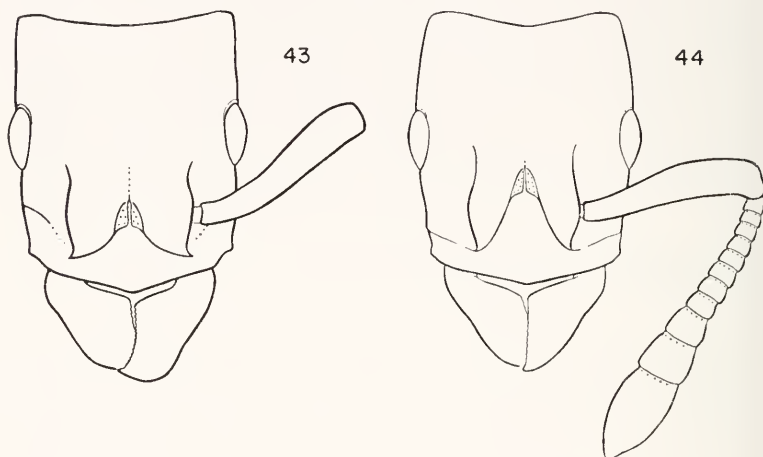
[58] GNAMPTOGENYS CHAPMANI sp. nov.

(Figures 19, 44)

Holotype worker: TL 3.4, HL 0.71, HW 0.56 (CI 79), L head with closed mandibles 0.93, scape L 0.47, greatest diameter of eye 0.17, WL 1.04, petiole L 0.38 mm.

Head as shown in Figure 44. Extremities of occipital angles rather sharply rounded and laterally compressed, but in side view not forming distinct "ears" as in *costata* and *menadensis*. Masticatory borders of mandibles feebly crenulate, almost straight. Alitrunk subcylindrical, only slightly narrower than head, tapering only slightly from front to rear. Humeri bluntly

subangulate seen from above; dorsal sutures of alitrunk obliterated. In lateral view, dorsal profile gently convex, almost straight in central portion, falling off through a sharper curve to the almost vertical upper part of the propodeal declivity (Fig. 19), which is marginate above and on the sides, but



Figures 43 and 44. *Gnampptogenys* spp., workers, full-face view of head. Fig. 43, *G. kalabiti* sp. nov., paratype. Fig. 44, *G. chapmani* sp. nov., holotype.

there are no propodeal teeth. The node is also shown in the figure; seen from above, it is widest behind, and slightly wider than long. Gaster slender, the first segment (postpetiole) truncate in front, slightly wider than long. Second segment longer than the first, but slightly narrower, strongly downcurved. Apical segments retractile.

Integument smooth and shining, with abundant round foveolae spaced on dorsum of head, becoming more crowded and finally contiguous on sides and gula; numerous but separated on alitrunk dorsum, very few on sides; few on sides of petiolar node and succeeding segment, becoming fewer and obsolescent on dorsal surfaces of these segments. Second and apical gastric segments, undersurface of first, propodeal declivity, sides of alitrunk, scapes, legs and mandibles predominantly smooth and shining, with occasional coarse punctures, especially on mandibles.

Fairly abundant erect fine hairs of uneven length over most surfaces of body, becoming more frequently reclinate on appendages and mandibles. Color brownish red; mandibles, legs and antennae yellowish.

Holotype [MCZ] taken by Dr. J. W. Chapman near his vacation home, Camp Lookout (altitude about 600 m.), in the Cuernos Mts., near Dumaguete, Negros Oriental, Philippine Islands, on March 19, 1924.

Paratype workers: two workers taken with the holotype; one worker taken with the female paratype (see below) at or near the type locality, on April 27, 1924 (J. W. Chapman leg.); two workers from Romblon Island, Philippines, April 5, 1924 (L. Morato leg.). Dr. Chapman thinks that the Cuernos Mts. collections came from nests in rotting wood in rain forest ravines. The paratype workers range downward in size from the holotype to one of the two specimens from Romblon: TL 3.0, HL 0.66, HW 0.48 (CI 74), WL 0.90, petiole L 0.35 mm. In smaller specimens, the head is disproportionately narrower, and even more noticeably so is the petiole; in the smallest specimens, the node is distinctly longer than broad; in these same specimens also, the foveolae of the sculpture tend to be smaller and farther apart. The shape of the occipital concavity varies slightly by individuals. In some workers and the female, the margins of the propodeal declivity form a distinct angle with the dorsum, in some the angle being almost like a blunt tooth or tubercle.

Female paratype, dealate: Size and proportions much as in larger workers, but alitrunk a little more robust and with flight sclerites differentiated in normal (but minimal) queen fashion; wing stumps present. Compound eyes only very slightly larger than in worker of same size; ocelli modest in size, but distinct.

G. chapmani is close to *G. laevior* Forel, but is much smaller and much lighter in (full adult) color than any of the *laevior* specimens I have seen; also, *laevior* has the node slightly longer than broad, a circumstance that is reached only in the smaller workers of *chapmani*.

[59]

GNAMPTOGENYS KALABIT sp. nov.

(Figure 43)

Holotype worker: TL 5.0, HL 1.06, HW 0.84 (CI 79), L head with closed mandibles 1.37, scape L 0.76, greatest diameter of eye 0.24, WL 1.47, petiole L 0.62 mm. Head as shown in Figure 43; note the almost perfectly straight and parallel sides and the rather sharp occipital angles. Seen from the side, the occipital corner is rather sharply rounded and margined by a narrow translucent border or carina, but no distinct "ear" is formed. Antennal scapes do not quite reach occipital angles, but reach the occipital border when laid straight back from their insertions. Clypeus not or very indistinctly sulcate in the middle; mandibles denticulate. Antennal funiculus stout, median segments very short, only about half as long as broad; last three segments forming an indistinct club; only the first and apical funicular segments longer than broad.

Alitrunk seen from above with obtusely angled (vertically margined) humeri; inferior border of pronotum forming a salient right angle in front of each fore coxa. Seen from the side, the alitrunk is deeper and a little more convex dorsally than in *chapmani*, but the conformation of the propodeum is similar. Coxal tooth acute but subconical, with broad base. Petiolar node paniform, of the general form of *costata*, *menadensis* and *chapmani*, slightly longer than high, with rounded dorsal surface; seen from above, node about as broad as long, narrowed anteriorly. Ventral process with posterior border sloping back gradually from an obtuse posterior angle. Base of postpetiole subtruncate (more rounded than in *chapmani*); postpetiole slightly broader than long; succeeding segment considerably longer and slightly narrower, strongly downcurved. Middle and hind tibiae each with a single slender, very minutely denticulate or subpectinate spur; all tarsal claws with a single extra strong subbasal tooth.

Head covered with deep, circular, umbilicate shining-bottomed foveolae, the ridges separating these forming a coarse reticulum; cervical surface of occiput smooth and shining, with a few fine striae in the middle; clypeus coarsely longitudinally striate, foveolate along sides of triangular median lobe; mandibles

smooth, shining, coarsely punctate. Alitrunk, petiole and sides of postpetiole with conspicuous, shining, mostly separated foveolae, still more widely separated over the postpetiolar dorsum (disc). The following areas smooth and shining: a median mesonotal-propodeal strip, metathoracic portion of sides of alitrunk, propodeal declivity, a small area on the nodal summit, the broad interfoveolar spaces on the postpetiolar dorsum, tergum of the second segment (except for posterior and lateral margins), and the apical segments of the gaster. Scapes and legs smooth and shining, with scattered punctures. There is also a superficial fine sculpture, characteristic of this species, found on the alitrunk, node and sides of the first two gastric segments in those interfoveolar spaces that are not smooth and shining. This fine sculpture ranges from a fine striation to a broken striolation or even to a finely coriaceous or reticulo-punctulate condition, the extremes grading through all intermediate substrate stages. This sculpture is more arched-striate and weakly shining on the disc of the pronotum and on the petiolar node; obliquely substrate or striate on the sides of the alitrunk and on the lateral and latero-ventral surfaces of the gaster, which are subopaque, especially the sides of the postpetiole; transversely striolate along the posterior marginal band of the postpetiole. Fore coxae transversely striate, middle and hind coxae densely and finely punctulate, opaque, pubescent. Sternum of postpetiole more or less smooth and shining in the middle. Pilosity, etc. much as in *chapmani*. Color medium brownish-red; antennae and legs more yellowish.

Holotype [MCZ] one of a nest series labeled, "Kalabit Country/N. Borneo/E. Mjöberg/ 3000 ft."

Paratype workers: 13 workers from type nest series: TL 4.6-5.3, HL 1.00-1.12, HW 0.79-0.90 (CI 79-80), WL 1.37-1.56 mm. Variation in form and sculpture is very slight. In some specimens, the ventral process of the petiole is a rounded lobe; in some, the occipital concavity is a little more or less broad and rounded than in the holotype.

Paratype female, dealate (from type nest series): TL 5.7, HL 1.08, HW 0.88 (CI 82), L head with mandibles 1.40, scape L 0.78, greatest diameter of compound eye 0.29, WL 1.73 mm. Alitrunk bulky, normal flight sclerites and wing sclerites present.

Mesonotum longitudinally rugose-foveolate; propodeal dorsum smooth and shining in the middle. Ocelli small but distinct, each with an adjacent blackened callus.

Males, 2 specimens from holotype nest series, of which one was measured: TL without genital capsule 4.9, forewing length ca. 3.8, HL 0.76, HW including compound eyes 0.87, WL 1.54, petiole L 0.52 mm. Antennal segment lengths: scape 0.38, funiculus I 0.15, fun. II 0.22, fun. III 0.21 mm. Occipital margin broadly and shallowly concave in the middle as seen full-face. Mandibles finely dentate, with the clypeus finely and indistinctly striolate, the mandibles and anterior clypeal apron longitudinally, remainder of clypeus transversely striolate. A strong median carina connects clypeus to anterior ocellus. Ocelli large, clear, separated by their own diameters or a little more. Compound eye large and rounded, greatest diameter 0.31 mm. Dorsum of head with distinct, circular, contiguous to subcontiguous foveolae; interfoveolar ridges forming a reticulum. Pronotum sculpture like head, but smooth and shining in the middle; scutum smooth, shining, with scattered foveolae; notauli very distinct, complete, coarsely foveolate. Scutellum rugose-foveolate. Propodeum smooth, shining along anterior margin and in center of declivity; elsewhere rugulose, weakly shining. Sides of mesothorax smooth to obscurely striolate, shining. Node smooth and shining above, foveolate laterally. Gaster and legs smooth, shining, with scattered punctures. Wings with venation as in *macretes* male [61]; microtrichiae yellow-tan. Color piceous to black; gaster, legs and antennae more reddish or brownish, genitalia yellowish.

Larva described and figured by G. C. and J. Wheeler (1952a: 122-123, pl. 3, figs. 1-8) as *Stictoponera* sp. This species is easily recognized by means of its rectangular head and substriate interfoveolar sculpture, especially of the sides of the postpetiole.

[60]

GNAMPTOGENYS GRAMMODES sp. nov.

(Figure 41)

Holotype worker: TL 4.9, HL 1.09, HW without eyes 0.93 (CI 85), L head with closed mandibles 1.44, scape L 0.97, greatest diameter of eye 0.28, WL 1.56, petiole L 0.52 mm.

Head shape as shown in Figure 41, drawn from a paratype, except that in the holotype the occipital border is a trifle flatter and longer, and the occipital angles not quite so gently rounded to the compound eyes. Seen in side view, occipital lobe rounded, but with a small, thin, subrectangularly rounded lamina or "ear" on the curve.

Alitrunk much as in the other medium- and large-sized Old World *Gnamptogenys*, convex, but the humeral angles rounded, with scarcely a trace of the corners prominent in *menadensis* and relatives. Promesosuture marked by a faint line; mesonotum with a narrow but deep and well-defined median longitudinal sulcus; metanotal groove fairly well marked, and the alitruneal dorsum slightly impressed in this region. Propodeum convex above and rounded evenly into the declivity, the latter short, feebly concave, bounded above and laterally by indistinct margins, and guarded on each side by a very small, rectangular to subacute vestige of a tooth. Coxal tooth slender, tapered to a blunt point. All tarsal claws with well-developed subbasal teeth.

Petiolar node paniform, shaped much as in the *menadensis* group, but with the ventral process reduced to a very small anterior tooth, directed obliquely downward and forward; node seen from the side a little longer than high; seen from above just about as long as it is broad; greatest breadth at about the posterior third. Gaster much as in *menadensis*; second segment perhaps a little shorter relative to first, but still long and strongly downcurved.

Apical borders of mandibles finely denticulate; shining, striate and with scattered punctures. Clypeus shining, with large punctures behind and short longitudinal rugulae in front; bisected by a narrow, deep longitudinal sulcus with shining bottom. Head with circular, shining-bottomed foveolae numerous, smaller in the median dorsal region, where they are mixed with longitudinal striation; larger and contiguous on the sides and beneath. Alitrunk covered with large, circular, shining foveolae, mostly contiguous above, becoming smaller and separated on the sides; in the metanotal area, the foveolae are mixed with some indistinct transverse striation. Interfoveal spaces here, especially a postero-median triangular area on the pronotum, smooth and shining, as is also the upper part of the propodeal declivity. Metapleura

and lower declivity with a few coarse horizontal striae. Node of petiole smooth and shining, with a few separated, shallow foveolae scattered over its surface; a few indistinct transverse rugulae or coarse striae across the lower anterior face of node. First gastric segment rather irregularly costulate or coarsely striate, with coarse, elongate punctures interspersed, transversely, across the basal third, longitudinally over the remainder of the dorsum, becoming a little smoother along the lateral margins. Sternum of first segment smoother, shining, loosely rugulose in a transverse direction and with large shallow foveolae. Second segment mostly smooth and shining discal, with small scattered punctures, although this smooth area is bordered along both side margins and in the posterior corners by short costal remnants with large punctures; along the anterior border there is a narrow band of transverse striation, followed by a brief zone of longitudinal costulation with coarse punctures or foveolae, extending about $\frac{1}{5}$ to $\frac{1}{4}$ the length of the segment. The sternum of the second segment is rugoso-punctate. Apical segments retracted in holotype, but these are smooth and shining in a paratype worker. Coxae of middle and hind legs finely punctulate, subopaque, as are also the antennal funiculi and the tarsi. Anterior coxae finely and closely striate horizontally, shining. Femora, tibiae and scapes smooth and shining, the scapes with one or two fine longitudinal rugae on inner and outer margins.

Body generally with abundant long, tapered, erect hairs, mostly 0.15-0.20 mm. long, becoming shorter, more nearly decumbent and denser on the extremities, including a dense brush on the gastric apex.

Color reddish piceous, almost black to the naked eye; antennae and legs light red.

Holotype [MCZ] a worker from Bisianumu, near Sogeri, Papua, at about 500 m. altitude, from a small colony or colony fragment nesting in a piece of rotten wood on the forest floor (E. O. Wilson leg., No. 671, March 15-20, 1955). Paratypes consist of 8 additional workers from collection No. 671 with the holotype, plus a stray worker, No. 655, taken from a rotten log in which lived a dealate female of *G. macretes* as well as colonies of *Pheidole* and *Cardiocondyla*, at the same locality as the holotype nest series. Size variation was relatively slight: HL 1.04-1.12, TL

4.7-5.1 mm. In some specimens, the occipital border is more evenly rounded (Fig. 41) than in the holotype, the clypeus is more sharply striate, even within the sulcus, and the propodeal teeth may be either more acute and more dorsally directed, or smaller and more obtuse, scarcely distinguishable from the sculpture. The transverse costulation of the first gastric segment may extend back over nearly half of the tergum of the segment, and in some specimens there are rather wide, shining spaces between some costulae. The distinctness and extent of the bordering remnant sculpture on the second gastric segment is also very variable, in some examples being almost completely obsolete, so that the entire tergum is smooth and shining, with only the scattered piligerous punctures to mar the surface. The color of the callows is dull yellow, and all intergradations of pigmentation occur in nest series No. 671, from yellow through brownish-red to nearly black. The legs are usually conspicuously lighter and more reddish or yellowish than the rest of the body. The female and male are unknown.

[61] GNAMPTOGENYS MACRETES sp. nov.

Holotype worker: TL 5.3, HL 1.25, HW 1.07 (CI 86), L head with closed mandibles 1.67, scape L 1.20, greatest diameter of eye 0.31, WL 1.90, petiole L 0.62 mm.

Very similar to *grammodes*, but larger overall and with a finer, more regular and more extensive striate or costulate component of the sculpture. Head shape as in *grammodes*, but the occipital border a little more broadly transverse (more truncate) and with the concave section in the middle broader and shallower. Humeri more distinctly angulate as seen from above, rectangular. Ventral process of petiole broader and longer, averaging larger than the coxal tooth of the same specimen.

Sculptural differences: Foveolae of head averaging a trifle smaller, the spaces between longitudinally striate right out to the sides, curving above and behind the eyes and then running transversely across the gula. Dorsum of pronotum coarsely striate longitudinally between foveolae on its posterior half, especially in the middle, where a narrow sulcus is all that represents the broader smooth triangular space of *grammodes*. Mesonotum with interfoveolar rugae converging posteriad, transverse

along posterior margin, so as to form a U. Median sulcus here obscure, partitioned into a row of coarse foveolae. Sides of alitrunk sculptured much as in *grammodes*; propodeal declivity very short, smooth and shining. Petiolar node shining, coarsely transversely striate, with a few scattered shallow foveolae. First gastric segment (postpetiole) evenly and distinctly striate or costulate (more finely and densely than in *grammodes*), transverse across the anterior quarter of the tergum, arching over the longitudinally-oriented remainder, with coarse interspersed punctures. The sides of this segment are smooth and shining, with sparse coarse foveolae. Second segment somewhat more finely striate longitudinally, with interspersed punctures, the striae reaching nearly half the length of the segment in the middle. A small anteromedian sliver, separated from the remainder of the surface by a curved line resembling the mark left by pressing a fingernail into something soft, is delicately transversely striate. Sides and posterior half of this tergal surface smooth and shining, with scattered piligerous punctures. Sternum of first segment predominantly smooth, with a few indistinct transverse wrinkles and grooves, shining. Sternum of second segment shining, indistinctly obliquely striate over the triangular side pieces. Sculpture otherwise as in *grammodes*, except that tarsi are only sparsely punctulate and are shining, and mandibles and clypeus more distinctly and more completely striate, including median clypeal sulcus.

Color brownish-red; mandibles, antennae and legs yellowish. The darker-colored parts of the body, especially alitrunk and gaster, overlain with a feeble pinkish-violet to bluish metallescence as viewed in certain lights.

Holotype [MCZ] a worker from colony series of collection No. 649, taken at Bisianumu, Papua, the same locality from which came the types of *grammodes* (see above), by E. O. Wilson.

Paratypes: 6 workers from the holotype nest series (No. 649): TL 5.2-5.4, HL 1.21-1.28, HW 1.04-1.11 mm. (CI 86-87). These specimens vary slightly in density of sculpture (especially on the petiolar node), in size of ventral petiolar process, and in striation of second gastric segment, which in some examples reaches, and even surpasses, the midlength of the segment. Some specimens have the occipital border straight or nearly so, seen full-face.

Paratypes: 3 dealate females — 2 from the holotype nest series, and a unique (Collection No. 655) taken from a rotten log in which a *G. grammodes* worker was also taken (see under *grammodes* paratypes, above) at Bisiamunu by Wilson. TL 6.7-6.8, HL 1.27-1.29, HW 1.11-1.12 (CI 87 in all 3 specimens), scape L 1.22-1.23, greatest diameter of eye ca. 0.35, WL 2.2, petiole L 0.65-0.66 mm. Alitrunk bulky; mesonotum foveolate, with longitudinal rugae between. Pronotum coarsely foveolate, the interspaces smooth and shining, especially at midline; sides of alitrunk behind pronotum predominantly coarsely longitudinally striate. Color darker than worker, mahogany, nearly black to naked eye; legs, scapes reddish-yellow.

Males, 3 specimens for holotype nest series, of which only one was measured: TL without genital capsule 6.0, forewing L ca. 4.2, HL 0.86, HW including compound eyes 0.98, WL 1.76, petiole L 0.52 mm. Antennal segment lengths: scape 0.33, funiculus I 0.14, fun. II 0.29, fun. III 0.29 mm. Mandibles triangular, finely dentate, with larger apical tooth. Mandibles and convex clypeus finely longitudinally striate. A strong median carina connects clypeus and anterior ocellus. Ocelli large, clear, separated from one another by a distance a little greater than the diameter of each. Compound eye large and strongly rounded, greatest diameter ca. 0.29 mm. Dorsum of head and alitrunk shallowly foveolate, with predominantly longitudinal rugae interspersed. Epimera convex, mostly smooth and shining, with a few foveolae. Propodeum steep, gently rounded, declivity not distinct from dorsum, unarmed, vermiculate-rugose. Petiolar node depressed-paniform, longer than broad and about half again as long as high, mainly smooth and shining, with a few scattered shallow foveolae; ventral process represented by a small oblique tooth or angle.

Gaster slender, smooth and shining, with piligerous punctures; an irregular transverse wrinkle or fold line across the tergum of the first segment in all of my specimens. Veins Mf2 and Rsf2-3 missing from forewing. Abundant long, fine, tapered erect hairs on most surfaces of body, becoming shorter and more decumbent on legs. Wings densely covered with brown microtrichiae. Color piceous to black, legs brown, trochanters and genitalia yellowish.

The holotype nest contained 30-40 workers and several males and dealate females; the colony was in a large rotting log in rainforest. Paratypes will be deposited in MCZ and elsewhere.

[62] *G. horui* is clearly a good species apart from *regularis*; *horui* is much smaller, and differs in other ways; besides, it is sympatric with *regularis* in the Guianas and probably elsewhere in South and Central America, but no intergrades between the two forms have yet been reported. The MCZ has numerous examples from each of several localities in British Guiana and the Panama Canal Zone, plus a sample each from Huachi, Rio Beni, Bolivia (W. M. Mann leg.) and from San Francisco, Brasso, Trinidad (A. E. Emerson leg.).

[63] The status of *Spaniopone haytiana* has been discussed in the main section of the generic revision as one of the *Holcopenera* Group of genera. See p. 218.

[64] *G. menozzii* is represented in the MCZ by type workers from Rio Grande do Sul, and by a worker from Volta, Parana: color blackish-brown, HL 1.16-1.21 mm., CI 109, 21-24 costulae between eyes. The ventral process of the petiole has a salient posterior corner, either digitiform or acutely dentiform. Two types of *G. schubarti* (Monte Alegre, São Paulo, 900 m.) are also blackish-brown, HL reaches 1.40 mm., but CI is still 109; 25-26 costulae between eyes. Ventral process of petiole with posterior corner reduced, obtusely rounded, shorter than anterior corner. A specimen similar to both foregoing species is from Corcovado, Rio de Janeiro (T. Barbour leg.): color bright ferruginous (probably teneral), HL 1.28 mm., CI 106; 22 or 23 costulae between the eyes. Ventral process of petiole with posterior corner obsolete, the process consisting only of the short, digitiform remnant of the anterior angle. It looks as though *menozzii*, *schubarti* and the Corcovado specimen may belong to one geographically variable species. More collections are needed.

[65] In 1896, when Emery first set up *Alfaria*, he included two species then new: a larger, very finely striolate one (*simulans*) and a smaller, opaquely and extremely finely subgranulose one (*minuta*). Since then, other authors have added six species to *Alfaria*. In addition, Maun's *Opisthoscaphus scabrosus* is clearly a member of the same group, and thus makes seven additions since the original description of the first two species.

Bufo is close to *simulans*, and in fact resembles in nearly every particular moderate-sized dark brown *simulans* specimens from Costa Rica; the *simulans* types I have seen are somewhat larger and are dull yellowish in color, but they may be teneral. The only clear difference shown by *bufo* is the well-developed metanotal groove in Mann's unique type, which conceivably could be an ergatoid female or some other departure from the true worker caste. Until we know more about the normal variation in *simulans*, it seems best to recognize the Mexican *bufo* as a species apart.

Five of the six other post-Emery species all appear to merge into a single variable species indistinguishable from *minuta*. This has been determined from careful comparison of types (except *mus*) one against another and against what little other material could be assembled. To begin with the final and most important check: Wilson has compared the types of *A. minuta* and *A. emeryi* found in the Forel Collection, and in turn matched these with a topotypic worker of *panamensis* that I had previously checked directly against a *panamensis* cotype, *carinata* cotypes, and the holotype of *O. scabrosus*, as well as additional samples from southeastern Brazil and Costa Rica sent by Father Borgmeier. Although there is some variation in size and sculpture, particularly of the gaster, these samples all appear to represent one species, *minuta*, which ranges from Central America to Bolivia and southern Brazil. The integument of this species is frequently fouled with a whitish incrustation, apparently a dried secretion like that found on many dacetines; this deposit very deceptively alters the appearance of the surface features, and can make even nest mates look very different.

Examinations of the *O. scabrosus* holotype [USNM] reveals that this genus and species was described on the basis of the artist's unrepresentative depiction of the mandibles, rather than from the specimen itself. Actually, the mandibles are in no way unusual for *minuta*. Most of the differences cited in the other species descriptions are based on small errors of observation or differences in viewing planes. The type review showed these distinctions to be non-existent or completely trivial. Though the *mus* type was not seen, the description tells enough to make this synonymy reasonably safe. The frontal groove mentioned by Santschi is undoubtedly the weak frontal carina as viewed in haste.

The most recently described species, Borgmeier's *striolata*, provides a link between the more "typical" *Alfaria* and the other *Gnamptogenys* species, and is itself a distinctive form.

[66]

GNAMPTOGENYS MECOTYLE sp. nov.

(Figure 42)

Holotype worker: TL 6.0, HL without cervical flange of occiput 1.16, HW 1.10 (CI 95), L head with closed mandibles 1.70, scape L 1.16, greatest diameter of eye 0.30, WL 1.85, petiole L 0.69 mm. General habitus of the larger species in the *G. rastrata* group, particularly *aculeaticorae*, *menozzii*, etc., but differing in the following respects.

(1) Scapes long, when laid straight back from insertions, surpassing occipital margin by more than $\frac{1}{4}$ their total exposed length; their dorsal surfaces coarsely longitudinally striate throughout.

(2) Costulation of head much less even, the costulae nearest the middle mostly much coarser than those near the eyes, mixed in gauge. Although a count is difficult and uncertain, it appears that there are about 28 costulae between the compound eyes, and about 11 between the frontal carinae. The longitudinal costulation of the clypeus is finer and regular.

(3) The longitudinal costulation of the alitrunk does not continue all the way forward to the anterior pronotal margin, but instead runs into an arched pattern across the anterior pronotum, where 5 or 6 costulae are transverse.

(4) Propodeal teeth (L. ca. 0.13 mm.) distinctly longer and broader at base than in *aculeaticorae*, and about $\frac{1}{3}$ as long as the distance between the centers of their bases. Propodeal declivity narrowed above, margined, smooth and shining.

(5) Node (Fig. 42) longer than deep and slightly longer than broad, gently arched, crossed by about 13 transverse costulae. Ventral process shallow, in the form of two short, blunt subequal teeth joined by a low concave lamina.

(6) Extreme base of postpetiole truncate in both dorsal and lateral views, leaving a small vertical anterior face that is nearly or completely smooth and shining. At the center of the border limiting this face above, the border is produced forward slightly as a blunt tubercle. Coarse costulae of postpetiole slightly wavy, becoming more wavy and erratic on sides of this segment near base.

(7) As minor characters, may be mentioned the cervical flange of the occiput, which is quite plainly visible in full-face view, and is convex in the middle; and the gula and postpetiolar sternum, both predominantly transversely costulate. Mandibles coarsely striate (smooth, punctate at apices) and weakly dentate along the masticatory borders. Color deep brownish-red; mandibles, antennae and legs more yellowish.

Holotype [USNM] taken by W. M. Mann on the lower Rio Madidi, Bolivia, in February, 1922. Four worker paratypes [USNM, MCZ, Coll. Borgmeier] taken with the holotype are similar, differing slightly in size, depth of color and sculptural details. The size ranges from that of the holotype up to that of a worker: TL 6.3, HL without cervical flange 1.22, HW 1.14 (CI 94), L head with closed mandibles 1.77, scape L 1.23, greatest diameter of eye 0.33, WL 1.96, petiole L 0.73 mm.

This distinct species is intermediate between *bispinosa* and *aculeaticoxae*, but is closer to the latter. It is apparently sympatric with *aculeaticoxae* at or near the *mecotyle* type locality.

[67] The variety *ericae* was based on a small Colombian specimen of *tornata* having the costulae on the propodeum, especially the declivity, longitudinal. Such specimens are commoner south of Guatemala, but Costa Rican and other series are found in which the patterns of this region are longitudinal, transverse, and intermediately U- or V-shaped, even in single nest series.

[68] The name *fiebrigi* applies to specimens from south of the Amazon (type locality is San Bernardino, Paraguay). I have seen material from Goias, Minas Gerais and São Paulo states with the shallower and more shining costulation and the less acutely bidentate ventral petiolar process described by Forel. The more northern of these series tend toward the "typical" *regularis* from Ecuador, British Guiana and Venezuela (in the MCZ). Var. *splendida* apparently applies to somewhat callow Mexican specimens. Samples in the MCZ come also from Costa Rica.

[69] *G. mordax* is a very variable species. Size and gastric sculpture are particularly unstable characters, but extremes of

variation are connected by intergrades both inter- and intranidally. From its description, it seems fairly certain that Latreille's *Formica nodosa* is the same as *mordax*. However, the name *nodosa* has not been used except in catalogs, and I believe that it should not replace *mordax*, which has been used for this common ant for nearly a century.

Forel's description of var. *purensis* applies well to one common variant of *mordax*, and I have examined a type of *sebastiani*, which is close to *mordax* types received from the British Museum.

[70] Specimens in the MCZ from Mexico (Guadalajara, Guerrero, Chiapas), as well as from Guatemala and Costa Rica, show that Santschi's differentiation of *curtula* and *stolli* as races is based on individual, partly allometric variation. Larger workers have transverse sutures on the posterodorsal alitrunk indicated as impressed lines. Apparently this species can live in somewhat drier places than the habitat of *G. strigata*, the related species having much the same range.

[71] In a nest series of *porcata* from Hamburg Farm, Costa Rica (F. Nevermann leg.), some specimens have the costulation of the posterodorsal alitrunk departing from a strictly longitudinal pattern; in one specimen, the propodeal area is covered by a well-developed whorl, approaching the condition as described by Santschi for the *magnifica* types. The distinction between *porcata* and *magnifica* is thus seriously weakened, and it may be that these two names represent a single relict species now in the process of being replaced by the centrifugally spreading relative, *G. pleurodon*.

[72] *G. pleurodon* is closely allied to *porcata*, but is smaller. It is widely distributed in the Amazon drainage. After examining the nidotype series from Bolivia of var. *recta* (USNM, MCZ), assigned by Santschi to *emeryi*, as well as a series from Yurac, 67 miles east of Tingo Maria, Peru (E. S. Ross and E. I. Schlinger leg.), I believe that the characters upon which Santschi differentiated *pleurodon*, *emeryi* and *recta* are individual or allometric variates that may be expected in almost any nest. Emery's

female *pleurodon* was separated as *vidua* by Santschi, but the differences are only those one might expect between worker and female of one species.

[73] *Gnamptogenys rastrata* group. This group is essentially the old subgenus *Parectatomma*. There exist in this group many uncertainties at the species level, due to the present scarcity of material, to the fact that several names were based on single specimens (and even these hardly adequately described), and to the circumstance that females are mostly not yet properly associated with workers. Some species must remain in doubt for the time being, but it seems wise here to review the material available and outline the problems involved.

G. rastrata. The type (NM Vienna) is a winged female from "Brasil/F. Sahlb. [erg]." HL 0.90, HL plus closed mandibles 1.40, HW including compound eyes 0.92, HW without eyes 0.83 mm. About 24 or 25 costulae between compound eyes: 9-10 between frontal carinae. Mandibles as in *menozzii* and *schubarti*, etc. (Fig. 16), masticatory border almost straight, feebly concave in basal third, faintly convex in mid third, then feebly concave again in apical third, showing a tendency toward the condition in *mediatrix*; no defined denticulation. Dorsal costulation of mandibles coarse, but not as bold as in *schubarti*, shading off to a shining, nearly smooth surface near the inner basal angle; costulation replaced by a smooth surface with shallow punctures on the apical third of the blade. Teeth of propodeum minute blunt tubercles; coxal tooth short, triangular, as in *schubarti* worker; shape of petiolar node and its ventral process also very much as in *schubarti* types, and like those of *aculaticoxae*. Costulae of petiole longitudinal, diverging behind as seen from above; transverse across anterior face of node. Color brownish red.

The worker from Alajuela, Costa Rica, determined by Emery as "*rostratum* Mayr" can scarcely be the same as the *rastrata* type from Emery's account, and considering the remoteness of the locality. For the present, I am unable to guess what Emery had from Costa Rica (Emery, 1890a:41).

Wheeler (1925:5) determined some specimens collected by Holmgren at Llinguipata, Peru, as *rastrata*, but I have examined four of these specimens and found them to be the form described by myself as *Holcaponera mina*, now placed in *Gnamptogenys* [46].

A worker in the collection of Father Thomas Borgmeier, from Nova Teutonia in southeastern Brazil, 300-500 m. altitude (F. Plaumann leg.) is close to *rastrata*, and may actually be its worker. HL 0.82, HW with compound eyes 0.86, HW without eyes 0.83 mm., 27-28 costulae between compound eyes. Eyes large. General habitus, mandibles, etc. about as expected for worker of *rastrata*, as compared with the female type. Petiolar node slightly but distinctly broader than long; costulae transverse across the anterior face; as seen from above, costulae longitudinal in the center, but around this concentrically circular, with only 2-3 transverse at the posterodorsal border. The ventral process is as in the type worker of *G. menozzii*, i.e., with concave ventral border, rounded anterior corner, and acute posterior corner. Color red-brown, head slightly darker than rest of body. The variation in nodal sculpture and form of ventral process of petiole may be normal for a single species; only further material will tell.

G. trigona. Emery described this form from a unique female from Novo Friburgo, Santa Caterina, Brazil. The description is in the form of a very brief comparison with *triangularis* Mayr; the size is "a little smaller . . . L. 4.5 mm." Sculpture much coarser than in *triangularis*; antennae thicker and shorter, the scape scarcely surpassing the occipital border. On the petiole, the costulation is disposed in concentric, but transverse, arches.

Except for the transversely concentric petiolar costulation, this characterization would match fairly well the type of *rastrata*; however, the petiolar sculpture may possibly be variable enough to include the *rastrata* and *trigona* patterns within one species. Other specimens I have seen, determined as *trigona* in various collections, are as large as or larger than *triangularis*, and have coarse costulation, but this is concentric on the petiole without being in the least transverse in orientation. I believe that these large specimens, such as the worker from Coreovado, discussed above [64], are probably not the true *trigona*.

I conclude for the present that *trigona* may be the female of the small species next described below, or else it is a synonym of *rastrata*.

Borgmeier Coll., Nr. 5756. Angra dos Reis, Rio de Janeiro State, Brazil (Lopes et Lent leg.). Four workers: HL 0.74-0.76, HW without compound eyes 0.69-0.73 mm., CI 93-96. Eyes large, but only feebly convex. 24-28 costulae between eyes. Mandibles as in *rastrata* type and the possible *rastrata* worker (Nova Teutonia, see above), but costulation coarse and extending more completely into basal corners. Propodeal teeth reduced to small tubercles, inconspicuous alongside the larger, protruding, obliquely-facing spiracles, just as in *menozzii*. Petiolar node about as broad as long; costulae concentric, forming a transversely elliptical pattern, variable in its center from specimen to specimen. Ventral process of petiole of the *menozzii* type. Teeth of posterior coxae shorter than in *menozzii*, but still digitiform or spiniform. Color red-brown. The total length of these specimens varies from about 3.1 mm. to 3.5 mm., outstretched with mandibles. This size is considerably less than the 4.5 mm. measurement Emery gave for the *trigona* female, and Emery's measurements usually fall under the ones I make on the same specimens of other ant species. Nevertheless, the correspondence of other characters, particularly the sculpture, with Emery's description, leaves the possibility open that Sample 5756 represents the worker caste of *trigona*.

G. triangularis. Four workers from: Ipiranga, S. Paulo State, Brazil (Luederwaldt leg.); Tafi Viejo (F. Silvestri leg.) and Tafecillo (N. Kusnezov leg.) in Tucumán, Argentina, measure HL 1.14-1.21, HW 1.12-1.16, eyes excluded. The head is variable in proportions, some specimens having the length slightly greater, others the width (CI 94-102). Only slight variation in gauge and density of costulation, from about 31 to about 35 costulae between the compound eyes. Propodeal teeth small but distinct and acute. Petiolar node varying from about as broad as long to distinctly broader than long, as seen from above more or less transversely costulate; sometimes only one or two transverse costulae in the middle, surrounded by concentric, ellipsoidal pattern on a transverse axis; sometimes the costulae transverse, meeting far down the sides of the node in a V or U pattern. Ventral process of petiole concave beneath, anterior corner rounded, posterior corner subrectangular. Color red-brown to blackish. Forel's race *richteri* reads like a common variant of *triangularis*, and it seems likely that Forel misidentified typical *triangularis*.

[74] Santschi's *reichenspergeri* is not a *Heteroponera*, to judge from a type worker, several males and a dealate female received from the Basel Museum and from Father Borgmeier. The frontal carina is lacking, and habitus and sculpture clearly place the species in *Gnamptogenys*, among the species of which *reichenspergeri* seems nearest to *relicta*. However, *reichenspergeri* has a well developed air of propodeal angles, and the striate sculpture of the alitruncal dorsum is effaced medially in the worker; the gastric sculpture is also largely effaced, broken up into short, bilaterally oblique sections of striation or fine rugulation, with large areas virtually smooth and definitely shining. The males are blackish in color, and generally resemble the species formerly placed in *Holcoponera*, but vein Rsf2·3 is present and situated as in *G. mordax* (Brown and Nutting, 1950, Pl. 8, fig. 5). The eyes of the worker are minute but distinct, and the promesonotal suture is cut through on the dorsum; the position of the metanotal groove is indicated by a faint impressed line. The petiolar node is anteroposteriorly compressed, and resembles those of *relicta* and the former *Spaniopone* and *Rhopalopone* species. Everything considered, this aberrant *Gnamptogenys* appears to be close to a perfect intermediate species linking the old genera *Gnamptogenys*, *Spaniopone*, *Holcoponera* and *Rhopalopone*.

[75] *G. rimulosa* is known only from the vicinity of Rio de Janeiro, where it is infrequently collected. Specimens sent by Father Borgmeier under this name agree well enough with the description.

[76] From the brief original characterization, *quitensis* is apparently only a minor variant of *tortuolosa*, which is widespread in Ecuador.

[77] GNAMPTOGENYS SEMIFEROX sp. nov.

(Figure 14)

Holotype worker: TL 7.0, HL 1.43, HW (across eyes) 1.44, HIW (at anterior corners) 1.39, closed mandibles extend about 0.81 mm., WL 1.99, petiole L 0.74, greatest eye diameter 0.29, scape L 1.11, absolute exposed length of left mandible 1.32; CI

97. Differs from *Gnamptogenys* (= *Emeryella*) *schmitti* workers of about the same size in its narrower head; shorter, broader, differently formed mandibles (Fig. 14); and in the longer petiolar node, which is a trifle longer than broad seen from above. The median clypeal lobe is more prominent, and its anterior border is entire and evenly convex in outline. The sculpture differs in a number of ways.

The costulation throughout, but particularly on the head and pronotum, is finer, less uniform and even, less shining, and a little less distinct. The interspersed punctation, very sparse and insignificant in *schmitti*, is more abundant, coarser and considerably more distinct in *semiferox*, especially on the head, but it still does not interfere seriously with the regularity of the costulation except in the areas just mesad of the compound eyes and on the dorsolateral surfaces of the propodeum. The punctures are mostly indistinctly bounded, but contain piligerous tubercles. The dorsal face of the propodeum is longitudinally and subvermiculately costulate (evenly and transversely in *schmitti*). Color deep piceous, as in fully pigmented *schmitti*, appearing black to the naked eye. The appendages are more reddish.

The holotype [MCZ] and two very similar paratypes [Coll. Borgmeier, MCZ] all bear the same data: Mt. Diego de Ocampo, 3000-4000 feet altitude, Dominican Republic, July, 1938 (P. J. Darlington leg.). Dr. Darlington tells me that the type locality was chiefly rain forest in which small palms were prominent, but that the land was being cleared for agriculture even at the time of his visit.

In the development of the mandibles, *semiferox* is intermediate between *schmitti* and *banksi* on the one hand and *mediatrix* sp. nov. on the other. In sculpture, *semiferox* is closest to *schmitti*, but shows tendencies toward the irregular, coarse, partly reticulate or punctate sculpture even better developed in *banksi*. In the lack of a dorsal tooth on the posterior coxa, and in the smooth postpetiolar sternum, *schmitti* and *semiferox* are alike and distinctive, but other *Gnamptogenys* lack the coxal armament, and *banksi* has a partly smooth postpetiolar sternum.

[78]

GNAMPTOGENYS MEDIATRIX sp. nov.

(Figure 15)

Holotype worker: TL 5.4, HL 1.04, HW (across eyes) 1.13, HW (near anterior corners) 1.08, closed mandibles extend about 0.53 mm., WL 1.64, petiole L 0.59, scape L 1.02, absolute exposed L of left mandible 0.88; CI 104. Very similar except in size and subfalcate form of mandible (Fig. 15) to *G. aculeaticoxae* and to *menozzii* and *schubarti*. Propodeal teeth short but subacute; coxal teeth very slender, with feebly clavate apices. Petiolar node broader than long and very nearly as long as high, its dorsal profile only feebly convex and only slightly higher posteriorly than in front (similar in shape to that of *aculeaticoxae*); anterior face steep, posterior face distinct and abruptly vertical (not distinct from dorsal convexity in *aculeaticoxae*). Subpetiolar process with both anterior and posterior free corners rounded, the latter obtuse, oblique ventral margin very feebly concave in outline, nearly straight (form of process as in *schubarti* types). Petiolar costulation predominantly transverse, as in *aculeaticoxae*.

Eyes large, convex, their anterior margins about at midlength of head. Costulation almost precisely as in *aculeaticoxae* samples from British Guiana so far as density and direction are concerned; 26-28 costulae between the eyes. Mandibles costulate on basal $\frac{2}{3}$, except near basal angles, where costulation becomes finer and then obsolescent; apical third of blade smooth, with coarse piligerous punctures. Color piceous, with reddish tinge; appendages lighter, more yellowish.

Holotype and one very similar paratype [MCZ and Coll. Borgmeier respectively] collected together at the present Belém do Pará, Brazil (Dr. Fred Baker leg.), presumably in the outskirts of the suburb of Souza (Mann, 1916:399).

Other paratypes are all from the environs of Rio de Janeiro [Coll. Borgmeier, MCZ]: 3 workers from "Rio de Janeiro" and one from the Jardim Botânico (H. Souza Lopes leg.); one alate female from Engenho Novo (C. R. Gonçalves). The workers vary somewhat in size, the largest being about the same size as the female in dimensions and proportions of the head. There is slight variation in the density of costulation and in the shape of the

subpetiolar process. The female is scarcely larger than the largest worker, and the eyes are only a little greater in diameter. HL 1.14, HW (near anterior corners) 1.21 mm. Forewing L 4.5 mm. Venation of typical *Gnamptogenys* pattern; Mf2 present but very short. Petiolar node a trifle shorter and broader than in the worker. CI 106.

[79] The material available to me, in conjunction with the discussions and figures of Santschi's 1929 revision, leads me to consider the names provisionally synonymized as representing parts of the continuous variation of one species. I have already discussed in general terms (Brown, 1957, pp. 489-490) the difficulties in Santschi's treatment of the variation of characters like gauge and density of costulation, body color, development of mesepisternal lobe or flange, and shape of ventral petiolar process; these very difficulties are most exaggerated in his handling of *striatula*, *brasiliensis* and relatives. From Santschi's own data, it seems unlikely that the types he saw of *striatula* and *brasiliensis* can be different species. But it seems possible that not all the infraspecific forms he described under *brasiliensis* also belong to the same species. Just what constitute species separations between *striatula*, the form with nominal priority, and other forms in or near this complex, we cannot yet say because of the lack of sufficient material and the inadequacy of detail in our knowledge of distributions of the various populations. In general, one might guess that most *striatula*-like specimens with more than 30 costulae between the compound eyes are *striatula* itself, while most with less than 30 are other, closely related species. An indication that this is so may be furnished on sympatric series from Agudos, S. Paulo State, Brazil (W. W. Kempf leg.), one of which is finely costulate (ca. 40 costulae between eyes) and has large eyes, while the other has smaller eyes and about 26-28 costulae between them. This latter type with coarser sculpture perhaps corresponds to the forms named by Santschi as *regularis*, *arcuata* and *rustica*, from southern Brazil and Paraguay, and may also be the same as the variant *simplicoides* of *brasiliensis*. At first view, there seems to be intergradation between the coarse and fine sculpture types, but this may be due in part to Santschi's inaccuracy in counting the

costulae (his counts are sometimes grossly contradictory as between key and text). Other intergradation in costular density may indicate that a character displacement situation exists between coarse and fine sculpture types when they occur sympatrically. The value of the eye diameter as a character has not been determined.

G. striatula is widespread in tropical South America, where the subpetiolar process usually or always has two rather distinct, subequal corners or lobes in its free portion. Specimens from Venezuela and Colombia look like *striatula*, but have the posterior corner or lobe much reduced, so that the process is more or less triangular or forms a single lobe, the condition characteristic of *G. curtula* [70]. The possibility should be entertained for the time being that *curtula* is the geographical variant of *striatula* in Central America and Mexico. In Costa Rica, there is a counterpart of the *rustica* group of South America in *wheeleri*, which maintains itself distinct from the *curtula* of Costa Rica in the form of the ventral process.

The relationship of *striatula* to *wasmanni* cannot be decided without more material; its node is rather thick and its ventral process subtriangular, so *wasmanni* seems to me to be closer to *pleurodon*.

The synonymy suggested and the opinions offered here concerning species-level relationships are strictly to be considered as "shooting from the hip," although it is felt that such treatment is justified at this time as a small beginning at making the necessary revision of the *striatula* group. It will perhaps be worthwhile reemphasizing for the benefit of future revisers the unreliability of one particular character given much weight by previous authors dealing with "*Holcaponera*" species. I refer to the mesepisternal lobe or flange. Not only is this structure highly variable in single nest series, but it has been very loosely dealt with by Santschi. Reviewing a substantial part of the same material, including unique types, that Santschi used in writing his revision of 1929, I have found that in several cases his drawings or descriptions are unrepresentative. For instance, his figure 19 shows the mesepisternal lobe of *wheeleri* with a small posterior portion that does not exist in the types; actually, it seems that Santschi was drawing a small ridge that traverses

the sternum at this level, and which can be seen by focusing down only slightly from the plane of the lobe. In other cases, the "tooth" at the posterior end of the lobe proved to be a stray bit of glue or dirt. In some series, the lobe was visible on only one side of one specimen; in the other specimens it was covered by glue or otherwise hidden. This means that Santschi's idea of the form and constancy of the lobe was usually drawn from a small fraction of the actual specimens he saw.

[80] *G. strigata* is a small, coarsely sculptured forest species. Wilson took it in rotten wood at Las Hamacas, near Santiago Tuxtla, Veracruz (tropical evergreen forest), and at Las Perlas, near Orizaba, at about 2000 m. in *Liquidambar*-hornbeam forest. C. and M. Goodnight took a specimen at about 1600 m. altitude in a pine grove at Union Juarez, Chiapas.

[81] *G. teffensis* is a large species for which we now have quite a few localities in the Amazon-Orinoco drainage, from the Guianas to Bolivia. The color is variable, but is most often some shade of ferruginous brown. The holotype of *teffensis* has been compared directly with the type of var. *concinna*, and in my opinion the two specimens fall within the normal variation of a single species; the posterior tooth of the *teffensis* type's mesepisternal lobe proved to be only a piece of dirt adhering to the lobe, and once cleaned, the lobe looks like that of *concinna*.

The very closely related *moelleri*, with its color variant *splendens*, has been recorded by specific locality only from the southeastern extremity of Brazil, particularly from Santa Caterina. Mann's Madeira-Mamore record applies to *teffensis*. Actually, *teffensis* and *moelleri* may be geographic strains of one species, although the more slender funicular segments of *moelleri* still seem to separate this form satisfactorily from *teffensis*, even considering that the funicular segments of *teffensis* are variable in thickness to some extent.

[82] *G. sulcata* is highly variable in color, and less so in density and gauge of its costulate sculpture. The principal color of worker and female ranges from uniform ferruginous (perhaps usually in callows) to black. The head is always dark in adults

near or past full coloration, and is piceous or black; the mandibles are always pale yellowish. The MCZ now has a number of series representing the stages of intergradation in both color and sculpture, and I have matched the types of *ypirangensis*, *bufonum* and var. *nitens* directly with these. Var. *lineata* has long been considered only a color variant of *sulcata*, and this follows the description well. Var. *cearensis* is described as a fine-sculpture form, and the details fit MCZ specimens well enough.

A male from Barro Colorado in the Panama Canal Zone (N. Banks leg.) is blackish in color, but has the pronotum a bright contrasting ferruginous yellow in hue. It is about the right size to fit workers of *sulcata* from the same locality, so I believe that it may well be the corresponding sex of this species.

[83] Just as Wheeler puts it, the only important difference (size) between the *minor* syntype series and the *schmitti* workers taken by Mann at Diquini, Haiti, is an "average" one. Differences between Forel's type and later collections are not apparent from Forel's description. Normal size variation is clearly great even within single limited series. Internidal size and sculpture variation is stronger in this than in some other *Gnamptogenys* species, but not as strong as, for instance, in *mordax*.

[84] Kennedy and Talbot (1939) claimed for the worker-female of *P. silaceum* one-segmented maxillary palpi, but their figures 9, 10 and 12 show that these palpi have two segments—a flattened apical one and a short basal one. The labial palpi were depicted with two elongate segments. This pattern has been found also in dissections of *croceum* and *relictum*; the maxillary palp of the former is shown in Figure 26. The arrangement of the first and second segments, with the second segment attached to the first by a slender lateral neck, holds through all of the species for which palpi have been examined, and is apparently characteristic of the genus.

Kratochvíl (1944) shows the palpi of worker *melinum* (under the name *fialai*) in his figures 2a, 2b, and these are like the sample of *pergandei* I dissected, with a formula of 4, 3, the apical segments being fairly elongate in form. The holotype of *stictum*, viewed without dissection, shows three exposed segments

for the maxillary palpus, the basal one evidently corresponding well to the second segment of the foregoing species; from this, I assume that *stictum* has four-segmented maxillary palpi, although the labial palpi of this species cannot be made out.

A single female of *micrommatum* dissected had two segments in the labial palps, while the maxillary palps appeared to have three segments on the right side, and two on the left. The two-segmented palpus has resulted from what seems to be a fusion of the basal segment with the slender basal neck of segment II. This condition may be an anomaly for the species; only further material will settle this.

According to Kennedy and Talbot (*loc. cit.*), the male of *silaceum* has a formula of 4,2, but here again their figures show that they did not count the small basal segment of the maxillary palpus. The formula is actually 5,2 as interpreted from their figures, and the second segment of the maxillary palpus is formed in much the same way as in the worker and female. We should expect that the formula for other species of *Proceratium* males is ordinarily 5,3 or 5,2.

[85] The distinctions drawn between the southern European *mayri* and the North African *algiricum* do not appear to be very striking. I have not seen any North African specimens referable to either species, but judging from the characters cited in the literature, it would seem that *algiricum* merely represents geographical variation of the European species. Final decision in this case must wait for critical comparison of the available material.

[86] Dr. George Arnold has kindly sketched for me the type worker of *arnoldi*, and I have presented these drawings here (Figs. 1, 34, 35) with the realization that they are perhaps not strictly comparable with the remainder of the figures of the genus given here. Undoubtedly Dr. Arnold and I have emphasized different points in a slightly different fashion, and, of course, the scale is not the same.

[87] *P. californicum* was described by Cook on the basis of a male stated to have been taken by himself at Glenwood in the Santa Cruz Mountains of coastal California. The description and figure fit well enough a *Proceratium*, but of course so few males are known in the genus that this stray specimen cannot easily be compared with any other species. This is the only record of a *Proceratium* from west of the Great Plains in North America north of Mexico. The type locality is not an impossible one by any means; undoubtedly the mountains of California still hold some surprises for ant collectors. Nevertheless, it would be well to confirm the presence of *Proceratium* in California through further collections before this record is unreservedly accepted, especially since other data in Cook's book is open to some question (see reviews: Brown and Wilson, 1953; G. C. Wheeler, 1954; E. S. Ross, 1954).

[88] A series from the Cuernos Mts., near Dumaguete, Negros Oriental, Philippines (J. W. Chapman leg.) fits the diagnosis of *carinifrons* well enough. The relationship of this species to *longigaster* needs investigation.

[89] This species, closely related to *micrommatum*, lacks the median clypeal projection supposed to be characteristic of *Sysphincta*.

[90] I have examined a specimen of *P. itoi* through the courtesy of Dr. K. Yasumatsu; this example is from Setagaya, Tokyo (A. Haga leg.).

[91] Wilson has compared the type of *lombokense* with Philippine specimens of *carinifrons*; the latter are much smaller than *lombokense* — according to Wilson's rough guess, only about $\frac{1}{4}$ the bulk of the *lombokense* type.

[92] In the MCZ there is a dealate female of *mancum* from Quirigua, Guatemala (W. M. Wheeler leg.) and a worker labeled simply, "Guatemala."

[93] Roger's description of *micrommatum* was good for its time, and from certain aberrant features mentioned, especially the contiguous frontal carinae, its identity seems assured with specimens from the following localities: Barro Colorado I., Canal Zone (N. A. Weber leg.); the *cavernicola* type, from Chilibrillo Caves, Panama; from Soledad, Las Villas Prov., Cuba (H. B. Mills leg.); Chichicastle, Tabasco (F. Bonet leg.); and Pueblo Nuevo, near Tetzonapa, Veracruz, Mexico (E. O. Wilson leg.). *S. micrommatum* is apparently widespread but rare in circum-Caribbean lands. With the exception of the *cavernicola* type, the above specimens were all taken in soil-cover berlesates. Borgmeier (1957:118) has recently dealt fully with *P. micrommatum*; he concurs in synonymizing *cavernicola*.

[94] When Roger first described *melinum* from specimens in the Berlin Museum, he recorded them as having come from "Carolina," mentioning that they were "with" the specimens he made the types of *P. croceum*. In view of other evidence, it seems possible that the association of *melinum* and *croceum* specimens in the Berlin Museum may have been the reason why both of these species have been considered to be North American since Roger's time. The record might have come under serious doubt had not Wheeler (1905) reported *P. melinum* (as *Sysphincta melina*) from the collections of P. J. Schmitt, made in southwestern Pennsylvania; this Pennsylvania record has been repeated since (e.g., Creighton, 1950:42), but without anyone's having reviewed the specimens upon which the report was based. I have tried to locate the relevant specimens in all the major collections in the United States and Europe, as well as in Schmitt's collection, now at St. Vincent Archabbey, near Latrobe, Pennsylvania, but the only species I could find collected by Schmitt were *silaceum* and *pergandei* (among Pennsylvania-collected material). In view of the fact that Wheeler did not mention directly any specimens that he had examined and determined as *melinum*, and since no specimens can be found corresponding to this record, the record is open to question. To my knowledge, no one has taken *melinum* in North America for about a century. Of course, such negative evidence must not be over-emphasized; after all, *Discothyrea testacea* Roger, described from the same general area, has now

been rediscovered in the southeastern U. S. [103].

However, there is other evidence to be considered. *Melinum* belongs to a group not otherwise known from North America, but which is widespread in temperate Eurasia. In 1895, Emery published reasonably good figures of all castes of *melinum* from the types, and careful examination of these figures reveals no significant difference between the types and the species described by Forel in 1886, and later by Emery himself, as *europaea*. In my opinion, *melinum* and *europaea* represent one and the same species, regardless of where their types came from. Of course, I consider it most likely that the *melinum* types really were collected in Europe, and I do not believe the species occurs naturally in the United States. In view of the greater familiarity of the name *europaea*, it might seem best to attempt to conserve it despite the priority of *melinum*. However, the best characterization of the species up to recent times was that of Emery under the name *melinum* (1895a), and the name *melinum* has been used in numerous publications since. In this case, I favor the prior name.

The other *melinum* group members are *itoi* of Japan, *fialai* of central Europe, and *rossica* of southern Russia. The last two seem to me to be slight geographical variants of *melinum* that are not worth formal names. The characterizations are based on scanty material, and little allowance is made for normal variation within series of "typical" *melinum*, which includes specimens with more convex alitruncal profiles approaching the condition as described and figured for *fialai* and *rossica*. Kratochvíl shows clearly that in *fialai* the palpal formula is 4,3, probably the same for all *melinum*. I have examined a *fialai* eupototype or paratype through the kindness of Dr. K. Samšinak.

[95] From Santschi's characterizations of *numidicum* and *normandi*, it is not clear that the differences between them are worth species separation. I have not seen any North African material myself, but Wilson has kindly compared for me a specimen in the MCZ Collections (ex Finzi Coll.) from Tirana, Albania (Ravasini and Lona leg.), with a *numidicum* type in the Emery Collection at Genoa. Wilson states that the type has more abundant erect hairs on head and alitrunk than does the

Albanian specimen, a point which apparently also is supposed to distinguish *numidicum* from *normandi*. Probably future study will show that *normandi* represents only slight individual or internidal variation within one species, *numidicum*. The Albanian record is, I believe, the first from Europe for this species, and represents a very considerable range extension; older records are all North African.

[96] A specimen taken by Wilson in a mixture of rotten wood chips and soil between the buttresses of a rain forest tree at Tumnang, Mongi Watershed, 1500 m., Huon Peninsula, New Guinea, agrees well with Emery's description and with a type of Donisthorpe's *Ponera caeca* (nec *Ponera coeca* Santschi) that was compared directly, courtesy of Dr. E. S. Ross of the California Academy of Sciences. The type of Donisthorpe's species came from Maffin Bay, New Guinea.

A single specimen taken in rotten wood in rain forest at Malanda, 800 m., northern Queensland (W. L. Brown leg.), is similar to the Tumnang specimen in size and in its weak, more or less shining sculpture, but has the propodeum gently rounded into the declivity as seen from the side, with only the most obtuse trace of angulation; the color is also lighter, but color means little in this genus.

Another *Proceratium* worker was taken by myself in a small rotten log on the floor of second-growth, *Eucalyptus gigas*-dominated rain forest on the summit of Tamborine Mt., southeastern Queensland, at about 600 m. altitude. The Tamborine worker may well belong to a species apart from *papuanum*, for it is slightly larger than the Tumnang and Malanda specimens, and a little more robust in body build; the petiolar node is slightly lower and thicker, and the sculpture is definitely rougher and opaque over the head and alitrunk, subopaque over the post-petiole. I do not find it expedient to describe a new species from a unique worker in such a tightly-related and little-known group of the genus at this time. However, with the description of *P. stictum* sp. n. below [99] added to the above records, it is clear for the first time that *Proceratium* is represented rather well in eastern Australia, nearly or quite south to New South Wales, and that at least two, and possibly even three, species are included in the fauna.

[97] Several workers of *pergandei* were found by myself under a rock in rich mesophytic forest on Great Blue Hill, Milton, Massachusetts, the most northeasterly record for the species yet known. These workers were confined in a plaster nest for two weeks, but could not be induced to feed on various dissected fresh insects offered them; they finally died one at a time. Dr. Wilson tells me that Mr. D. W. Pfitzer of the University of Tennessee once told him that he had observed workers of *pergandei* clustered around a spider egg-case, into which they appeared to be trying to bite their way.

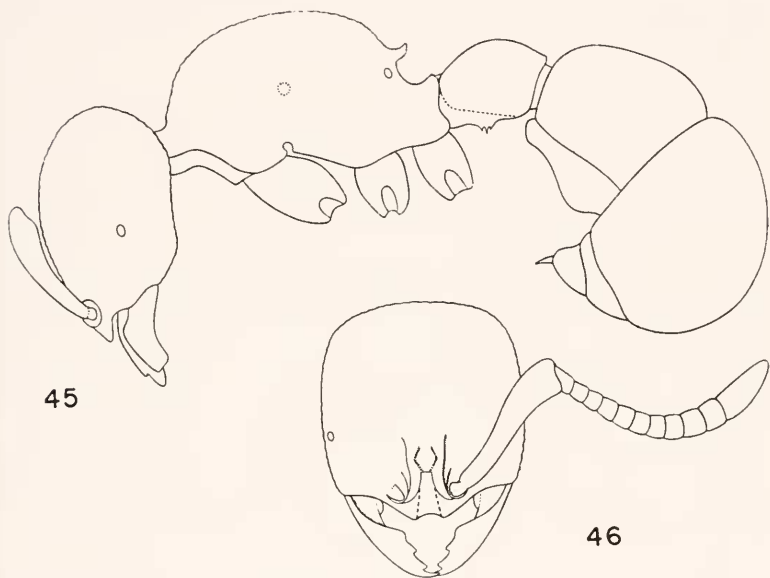
[98] *P. silaceum* is the common species of the genus in North America. Wilson and I have found it feeding on spider and other arthropod eggs in nature, and have maintained it on spider eggs almost exclusively for weeks in the artificial nest. When well supplied with spider eggs, it will have nothing to do with other insect remains, including eggs, larvae or pupae of other ant species, upon which the related species *croceum* was fed by Haskins (1930). In both natural and artificial nests so far examined, the *silaceum* workers tend to store more eggs than they will immediately need. *P. silaceum* ranges northward as far as Lexington and Woburn, Massachusetts, where I have found it extremely rare, nesting under stones. It nests under stones also in moist, wooded hilly sections of eastern Pennsylvania, but in the adjacent lowlands and pine barrens along the Delaware River and in New Jersey, the nests are almost invariably in rotten logs or stumps.

The synonymy of *silaceum*, long a source of confusion, was settled by Creighton in his penetrating study of 1950 (pp. 36-40); his conclusions are followed here.

[99] *PROCERATIUM STICTUM* sp. nov.
(Figures 45, 46)

Holotype worker: TL (to posterior curve of second gastric segment) 4.7, IIL 1.08, HW 0.97, WL (with cervix) 1.48 mm.; CI 90. The general form of the head and body is shown in Figures 45 and 46. Notable is the broad clypeus, separated from the remainder of the cranium by a reasonably distinct suture,

and not markedly tilted from the horizontal position. The broad median lobe is bicarinate, the space between the carinae concave and emarginate at the anterior border; this broad lobe corresponds to the much more strongly reduced median process in the *pergandei* and *melinum* group workers and females, and it may well be the homologue of the various modifications of the bicarinate or bidentate clypeus as found in *Monomorium* and many other myrmecine genera. Maxillary palpi with at least three segments (probably four); labial palpi not seen. Antennae 12-segmented, gently incrassate toward apex, not forming a distinct club, but the apical segment much longer and thicker than the rest.



Figures 45 and 46. *Proceratium stictum* sp. nov., holotype worker. Fig. 45, lateral view of head and body. Fig. 46, full-face view of head. Drawings by Dr. F. Y. Cheng.

Mandibles triangular, with oblique apical (masticatory) margins set with four coarse teeth counting the blunt basal angle. Eyes distinct but small, each with a single clear, convex facet, placed a little anterior to the cephalic midlength.

Alitrunk stout, compact, convex above, without traces of dorsal transverse sutures, seen from above broadest across the humeri. Propodeal teeth short but prominently projecting, dorso-ventrally flattened and with upturned apices. Propodeal declivity short and broad, not margined above or on sides between upper and lower (metapleural) teeth; the latter teeth broad, laterally compressed, subtriangular. Petiolar node low and paniform; seen from above slightly but distinctly longer than broad and very slightly narrowed in the anterior half, suggesting incipient formation of a peduncle; node anteriorly squarely truncate, with prominent anterodorsal angles opposing the mesial surfaces of the lower propodeal teeth; upper nodal surface evenly convex in both directions; ventral appendage divided into three small, acute teeth.

Basic sculpture of head, alitrunk, petiole and postpetiole densely and irregularly rugulose and with numerous well-spaced, narrow, but deepset punctures with central tubercles at their bottoms, this sculpture boldest on the petiole. Cephalic dorsum inside the eye with punctures indistinct, but the rugules more linear and running obliquely posterolaterad from the region of the antennal insertions; vertex with transverse rugulation. Cervical dorsum and lower propodeal declivity smooth and shining; first gastric segment also smooth and shining, but abundantly sown with small, distinct punctulae. Clypeus very finely rugulose. Mandibles very strongly striate up to apices, which are smooth, their bases with elongate punctures between striae. Legs and antennae very finely and densely punctulate, subopaque. (Legs stout, middle and posterior tibiae each with a single broadly pectinate spur; tarsal claws moderately well developed, simple, as in other *Proceratium* species.)

Pilosity fine and erect, moderately long and abundant, distributed evenly over the entire body, including mandibles, antennae, legs and gula. Pubescence fine, dense, suberect to subreclinate, but not hiding sculpture. Color rich ferruginous red; appendages, mandibles and apical segments of gaster yellowish-ferruginous.

Holotype [MCZ] a unique worker taken at Kuranda, northern Queensland, Australia, in a rotten log in heavy rain forest at an altitude of about 370 m., November 1, 1950 (W. L. Brown).

This species is abundantly distinct from the members of the *pergandei* and *micrommatum* groups, to which it is most similar. The broad median clypeal lobe, the form of the propodeum and its teeth, and the low, elongate petiolar node are key characters, all of which seem to be near the generalized type of the genus. The single-faceted eyes and solidly fused alitrunk are, however, as specialized as these structures ever become within the genus, except that the single facet of the eye, while hyaline, is somewhat larger than the eyes in some other species. It would be most interesting to see the winged sexes and the larva of this apparently very primitive *Proceratium*.

[100] The holotype of *P. toschii* has been examined through the kindness of Prof. Athos Goidanich. I have drawn the middle front section of the head (Fig. 25) and the petiolar node and adjacent segments (Fig. 30) from the holotype; the difference between my figure of the node and Consani's figure 1, no. 2, may be explained by the fact that Consani included in his drawing a large piece of dirt that adhered to the apex of the node and was matted in the hair, appearing to be a part of the node itself.

[101] The four species described from southern Australia are *bidens*, *crassicornis*, *leae* and *turtoni*. I have collected workers that compare well with the types of *turtoni* in the National Museum at Melbourne; these specimens come from the Dandenong and Warburton Ranges to the east of Melbourne, where the species is fairly common in the fern gullies as well as under stones in grassy-floored sclerophyll forest at 600-700 m. on the Dandenong summits. I am unable to separate this species, which varies somewhat in color of integument in the queens, from the type of *leae*, and I think that further study may prove them synonymous. The type of *bidens* in the MCZ is a large, dark-colored worker with fairly prominent propodeal angles or teeth that are directed obliquely upward, in this differing from the workers of *turtoni* I have seen. The *bidens* type, however, has a very faint trace left of the promesonotal suture across the alitruncal dorsum, and therefore it could be an ergatoid female. Thus, its specific identity with *turtoni* or *leae*, or with both, is not ruled out. The species *crassicornis*, retaken by W. M. Wheeler at Margaret

River in southwestern Australia, is smaller than *turtoni*, and, at least in the series before me, has eight-segmented antennae. Clark states that the antennae of his types had nine segments, but his figure 4 shows ten segments, indicating that he really did not have a clear count of the segments. The propodeal angles of *crassicornis* workers are also more prominent than are those of *turtoni*.

Clark told me personally in 1950 that he thought *turtoni* and *leae* were probably synonyms. The original collector of *bidens*, Mr. F. E. Wilson, informed me in a conversation that the real type locality of this species was Cement Creek, at about 700 m. altitude, and some miles up into the Warburton Range, away from the town of Warburton.

In addition to the species already discussed, I have found what appears to be another distinct species at One Tree Hill in the Dandenong Range, east of Melbourne. This species is smaller than *turtoni*, has less noticeable pubescence and more distinct propodeal angles, and has seven-segmented antennae (two worker specimens, antennae on both sides counted). I have considered that these differences might be due to allometry within a single species, and continuing to take allometry into account, it seems best to wait until all of the available Australian *Discothyrea* material can be examined in one place before attempting to decide the status of the seven-segmented variant. Most of this material, including some belonging to the MCZ, is still with the Clark Collection at Canberra.

[102] The African species of *Discothyrea* fall into two groups: those with the clypeo-frontal fusion process flat-topped and broad (Fig. 48) — *oculata*, *sculptior* and *mixta*; and those in which the process forms a simple convex or angular vertical plate — *traegaordhi*, *hewitti*, *poweri* and *patrizii*. In the first group, *mixta* is distinct by the characters mentioned in the description [105]. Santschi's *sculptior*, described as a variety of *oculata*, may in fact be no more than a variant of that species. I have not seen the types of either *oculata* or *sculptior*, although I have seen a single worker collected by N. A. Weber in Kenya that in most respects answers to the *oculata* description, except that the eyes have less than 30 facets.

In the second group, the species are apparently all very close, and they may, in fact, represent only a single species. *D. poweri*, with its twelve-segmented antennae, seems the most distinctive form, and possibly it is really distinct. Antennal segmentation is particularly dangerous to use as a species character in this group, since Santschi, in his original description of *traegaordhi*, mentioned that segmentation varied between eight and nine in this species, and he later admitted that he had seen balsam preparations of the same species with only six segments, "the others more or less fused and indefinable," according to Bruch (1919:400). The statement of Weber (1949:3) in differentiating *patrizii* is accordingly of little value; he states, "The eight-segmented antennae separate this species from nine-segmented *hewitti* Arnold, *oculata* Emery, and *traegaordhi* Emery [sic], as does also the smaller size. The lobate fused frontal carinae of *hewitti* are produced as a triangular plate." Santschi gave as the original measurement for *traegaordhi* worker, "Long. 1.5 mill.," while Weber gives 1.6 mm. as the length of his *patrizii* worker, so Weber's "smaller size" does not hold, from this information. *D. hewitti* differs from *traegaordhi* only in characters that usually differ between female and worker castes of the same species, so far as their respective descriptions go, so we cannot tell whether they are really distinct or not. The fronto-clypeal plate of these species is probably not so different as the characterizations indicate; the posterodorsal margin is probably always nearly straight and steep, while the anterior margin is broadly rounded. The plate could therefore be variously described as convex, rounded, or even "triangular," according to what feature of the outline is stressed. I have two workers that belong to this complex, which I shall call *D. traegaordhi* at least provisionally, from Ebolowe, Cameroons (A. I. Good).

[103] The New World species so far described number eight, seven of which are keyed by Borgmeier (1949:205); the eighth species was added by Borgmeier (1954:191); see also Borgmeier 1957:122. Smith and Wing (1954) have redescribed and discussed the type of the genus, *D. testacea*, from southeastern North America. Some of the species are described only from females, others only from workers, and the total material so far placed

under study is so small that the present arrangement cannot be considered close to final. In separating the species, too much reliance has been placed on antennal segmentation counts, which may be unstable in single species here as elsewhere; the comparative statements on total length are also suspect, because measurements of ants this small have been notoriously inaccurate, due to lack of standardization as well as to poor optical aids. Perhaps four to six good species are represented. A definitive study must await more material and re-examination of the types. One additional word of warning should be heeded in studying *Discothyrea* species, particularly the New World forms: it is entirely possible that some forms now established in the Americas are tramps originating in Africa or Asia. This possibility makes it imperative that the Old World forms all be duly considered in any New World study of the genus.

[104] *D. remingtoni* was described from a single worker from near La Foa, New Caledonia. Wilson has since collected two unique workers of this species or near it; one of these is larger than the type, the other is smaller; the larger specimen has the head as well as the alitrunk dark brown, while in the smaller one, the head is yellow and the alitrunk ferruginous. These specimens also show variation in the convexity of the alitruncal profile, and in the thickness and height of the petiolar node. They may or may not belong to the same species as *remingtoni*; with such limited material, it is impossible to decide. The larger specimen comes from Ciu, near Mt. Canala, 300 m., rain forest soil cover berlesate; the smaller worker is from Mt. Mou, at about 180 m., both localities in New Caledonia.

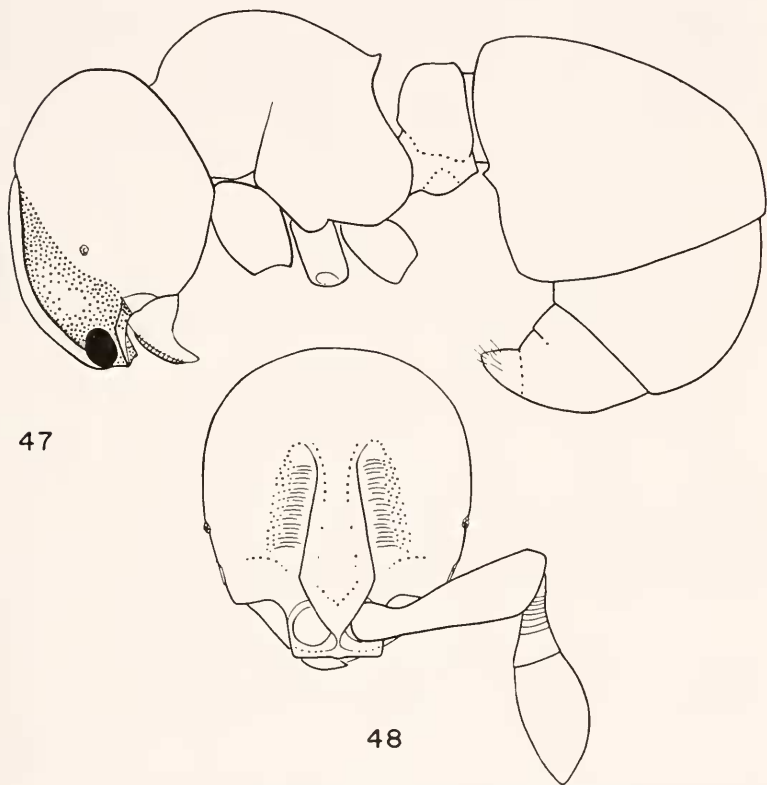
Another, much larger *Discothyrea* was taken by N. L. H. Krauss at an unspecified locality in southeastern New Caledonia (southeast of Noumea); this individual is 2-3 times the bulk of the workers, and has a faint sutural line behind the pronotum, indicating that it may be an ergatoid female. The eyes are larger, and the sculpture of the head is coarsely but shallowly punctate, with coriaceous intervals, the whole surface virtually opaque. This may be the ergatogyne of *remingtoni*, but if so, the caste differences are unusually strong in this species.

[105]

DISCOTHYREA MIXTA sp. nov.

(Figures 47, 48)

Holotype worker: TL 2.4, HL (without mandibles) 0.66, HW 0.59, WL 0.61, scape L 0.43, funiculus L 0.52 mm. Form of head and body shown in Figures 47 and 48. Similar to the species *D. velutina*, *D. bryanti* and *D. oculata*, particularly the last, but smaller in size and with smaller compound eyes. Funiculus



Figures 47 and 48. *Discothyrea mixta* sp. nov., paratype worker. Fig. 47, lateral view of head and body. Fig. 48, full-face view of head.

10-segmented, as determined from examination of two funiculi under compound microscope; median segments extremely short, not distinct on the intact specimen as viewed with reflected light.

Frontoclypeal platform narrower than in *oculata*, with slightly raised borders. Depressed scrobal areas distinct. Palpal segmentation undetermined. Propodeum concave, with a sharp concave margin above joining the propodeal angles, which are subrectangular as seen from above, though acute and dorsally inclined as seen from the side. Petiole thick disciform, as seen from above, truncate anteriorly and posterodorsal border without a distinct tooth or process. Postpetiole longer than broad, ovoid as seen from above, much larger than the succeeding segment.

Head and body densely and rather coarsely punctulate, the punctulae nearly or quite contiguous, but becoming a bit more spaced on the gaster. Scrobal depressions indistinctly and finely transversely striolate, becoming smooth and shining mesad. Mandibles and appendages very finely and superficially punctulate. Integument generally opaque, except for shining bottoms of scrobes and parts of the gastric dorsum, which are feebly shining in some lights.

Body, including mandibles and appendages, covered with dense, fine, very short, whitish decumbent pubescence, becoming more nearly erect on alitrunk, and obliterated from the shining parts of the scrobes.

Color medium ferruginous, appendages more yellowish.

Holotype [MCZ] one of five workers taken together at Bolahun, Liberia (J. C. Bequaert leg.). Paratypes [MCZ, USNM] are the four workers taken with the holotype, one of which has now been destroyed during the course of dissection. Varying only slightly in size, and scarcely at all in form, from the holotype. In the smallest workers (HL 0.63 mm.) the head tends to be a little narrower in proportion to its length, and the sides of the head may be a trifle more nearly straight. In some specimens, the occipital margin is a little straighter than as shown in the figure. Color varies from yellowish ferruginous to medium ferruginous. The lighter specimens show a more or less distinct pair of brownish-tinged longitudinal bands on the gastric dorsum; these may be internal structures showing through the integument.

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INDEX

Included here are names of ant species, genera and higher categories mentioned in the body of the paper. Names mentioned in the Appendix and captions to figures are excluded where direct reference is made to them through bracketed numbers at the primary reference. The pages of the primary references are given in bold face below. Abbreviations for generic names are as follows: Ac. = Acanthoponera, D. = Discothyrea, E. = Ectatomma, G. = Gnamplogenys, H. = Heteroponera, Pr. = Proceratium, R. = Rhytidoponera.

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